# The theory and use of methods for the study of mammalian palaeoecology.

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## Abstract

Palaeoecology is one way of reconstructing the palaeoenvironment. The ecological and theoretical foundations underlying a number of palaeoecological methods are discussed and these methods are then applied to mammalian faunas from the fossil record.

Three basic palaeoecological approaches are described: Indicator methods, population methods and community diversity methods. Ecological niche theory is used to relate these to neo-ecological concepts concerned with the distribution of species with respect to habitats and other species. Detailed consideration of the theory behind these approaches shows that indicator methods are only suited to recent faunas, while ancient faunas, and those containing large numbers of species, are best analysed using diversity methods.

Climatic climax vegetation types of tropical and temperate regions are described, together with examples of their associated mammal communities. Each habitat supports a community with a distinctive adaptational structure which is related to the productivity, stability and physical complexity of the habitat.

Palaeocommunities are often incompletely preserved, and the sensitivity of selected palaeoecological methods to species loss is tested in a series of simulations based on communities from known modern habitats. The results obtained form the basis for the interpretation of fossil faunas.

Mammalian faunas from the European Pleistocene sites of Lazaret and Westbury-sub-Mendip are analysed using several methods, and it is seen that even when a fauna is rich and well-identified, different methods give slightly different results. Further analysis of a large number of Pleistocene faunas shows that extinct habitats can also be identified.

The community structure of early Miocene faunas from East Africa is analysed and compared with modern tropical communities. It is concluded that the disappearance of the early Miocene hominoids and the subsequent radiation of the cercopithecines were part of a general change in the structure of African forest communities.

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# Section I

## Theoretical principles

# Chapter 1

# Introduction

## 1. Introduction to Palaeoecology.

During the last few decades an increasing amount of research has been given over to attempts to reconstruct palaeoenvironments, mainly as a means of providing an environmental context for the study of evolving communities and biological lineages. This is not least because the theory of Natural Selection predicts that the environment is very important in shaping the organisms that live in it. Largely because of the enormous interest in human evolution, which is to be found among academics and the general public alike, this trend has been especially evident in palaeoanthropology.

As a consequence of the increased interest in palaeoenvironments, palaeoecology has gradually assumed a greater importance within the field of palaeontology, and a variety of palaeoecological methods have come into use. While the proximate goal is usually a description of the environment in which the organisms lived, the ultimate goal of these methods is an understanding of the complex relations that existed between ancient organisms and their environments, usually to give an insight into the factors causing evolution or extinction. This study is intended to do two things, firstly to describe and investigate the relative merits of a number of palaeoecological methods when faced with

some of the problems posed by the mammalian fossil record, and secondly to illustrate how these methods can be used to fulfill some of the aims of palaeoecological analyses.

The research described relates specifically to mammalian palaeontology but most of the methods discussed below could be applied equally well to groups of organisms other than the mammals as long as basic biological differences between these groups are taken into account. Since the nature of the relationship between organism and environment varies between groups, the terms in which the environment is reconstructed will vary according to the limiting factors affecting the organisms chosen. For instance, plants are generally affected by regional climatic factors and variations in local microclimate and soils, whereas marine brachiopods can usually be associated with particular sedimentary facies. Similarly, the general ecology of most terrestrial mammals is influenced by the same kinds of environmental constraints. Thus, although this research has special reference to palaeoanthropology the methods described, and the conclusions reached, can be taken to apply to the palaeoecology of mammals in general.
It must be realised, however, that the success of the mammals is to a great extent due to their adaptability which in turn makes them less sensitive to environmental fluctuations than many invertebrates and plants.

Although invertebrates such as molluscs and insects, and plant remains including pollen are much better environmental indicators than mammals when they are present, mammals have the advantage of occurring more frequently in the fossil record, and of being perhaps the best studied terrestrial group throughout their evolutionary history.

a. Methods of Reconstructing Palaeoenvironments.

Most methods of investigating local palaeoenvironments are either geological or ecological in nature depending on whether they concentrate on fossil-containing sediments (including fossil soils), or on the fossils themselves. Where regional frameworks are sufficiently well developed, a considerable contribution can be made by knowledge of the regional palaeoclimatology and palaeogeography (see, for instance, Andrews & Van Couvering, 1975). Geological approaches to local palaeoenvironmental reconstruction involve the investigation of the geochemistry and form of sedimentary particles, as well as sedimentary structures and the fine structure of rocks, in an attempt to reconstruct depositional environments in terms of where the sediments originated from, and what processes have influenced them before, during, and after deposition. In some cases fossils may be treated as sedimentary particles and by this reasoning the study of taphonomy (literally - the laws of burial) can be

considered to be a geological rather than an ecological approach although in many cases it is an essential prerequisite to palaeoecological studies. Taphonomy is discussed in chapter 3 (see p. 97), however, since the research is concerned with palaeoecological methods, geological approaches will not be dealt with in any detail.

b. What is Palaeoecology?

Ecology is the study of the relationships between living organisms and their environments. These are relationships that concern strategies involved with eating, avoidance of being eaten, reproduction and so on, which govern the survival of the organism and its population in any natural environment and ultimately determine distribution and abundance. Palaeoecology is the study of the same relationships based on evidence drawn from the fossil record.. Thus, modern ecology and palaeoecology are basically the same; the main distinction lies in the fact that modern ecologists can observe directly and make quantitative measurements, whereas palaeoecologists can only infer the existence and nature of the relationships that concerned the animals they are dealing with. Compared with modern ecology, palaeoecology operates at a very simple level and very often palaeoecologists are trying to uncover the kinds of relationships that modern ecologists take more or less for granted.

Palaeoecology thus relies to a large extent on a firm foundation in neoecology, and it is unfortunate that the concepts of modern ecology are not easily converted into palaeoecological techniques. Because fossilization is so chancy, the most trustworthy data tend to carry little information (for instance, quantitative evidence is often unreliable or even impossible to obtain) and less informative data inevitably give rise to less informative results. For the same reason palaeoecological methods need only be as rigorous as the fossil data allow, and they are usually less rigorous than those used in modern ecological studies.

c. Why is Palaeoecology Important?

Palaeoenvironmental reconstructions have no inherent value of their own, they are important only as tools to other ends. Although palaeoecology can be used to provide time depth for modern ecological studies, its main justification lies in the fact that the theory of Natural Selection predicts that the environment, in one form or another, is of overwhelming importance in evolution, and the concept of adaptation necessarily implies the existence of conditions that must be adapted to. Morphological characters of individual species, the social structure and organization of populations, and even the structure of whole biological communities are all influenced by environmental conditions, thus when considering evolution through adaptation by natural

selection, and extinction through failure to adapt, some form of contextual evidence is essential. Arguments involving the concept of adaptation and the evolution of adaptive traits are incomplete without some mention of environmental conditions, and a knowledge of these conditions is an essential first stage to a full understanding of the evolutionary history of any organism or group of organisms being studied.

The fundamental importance of palaeoecology thus lies in the fact that it provides a means of obtaining information about the environmental conditions that prevailed in the past, and more importantly the relations of organisms to these conditions, thus enabling evolutionary hypotheses to be proposed in a way that makes them logically complete and testable.

d. What are the Aims of Palaeoecology?

From what has been said above it is obvious that the main aim of a palaeoecological analysis is to provide evidence about the palaeoenvironment and its inter-relations with the organisms associated with it. The environment of an organism in the broadest sense can be divided into two parts: The external environment consists of factors such as habitat, climatic influences, and competition and predation pressures from other organisms of the same and other species. All of these represent parts of the environment that may affect

"fitness", and thus in the long term the evolutionary future of the population and the species as a whole. Alongside this is what may be called the internal environment by which the functional systems of organisms are subject to the influences exerted by other functional systems. In this context parts of the organism itself form the environment of other parts of the organism. Although palaeoecology can cast very little light on this "internal environment", a considerable amount of evidence concerning the external environment can be obtained. For palaeoenvironmental studies in general, different methods of analysis enable the environment to be reconstructed in several different ways, and the type of reconstruction desired depends on the object of the study being undertaken. Where palaeoecology is concerned, the aim is usually one of the following:

i. Faunal and Community History.

The study of community evolution requires an environmental reconstruction in terms of the factors that control community composition and structure. These are mainly habitat structure and competition from other species both within and outside the community being studied. Community evolution can be related to the study of individual species and lineages, and all characteristically need a long time base and a wide geographical coverage.

ii. Lifestyle Reconstruction and Palaeobiology.

The study of the history of individual species in terms of evolution and its obverse, extinction, revolves around investigation of the environmental factors that affect species distributions (such as climate, vegetation, and competition from other species) and the lifestyle or palaeobiology of the species concerned. Such studies typically have a fairly long time base and span several sites.

iii. Prehistoric Economy.

Reconstruction of the way of life of species of special interest such as Pleistocene hominids is a special case of lifestyle reconstruction, which typically takes the form of an investigation of resource availability and prehistoric economy. The object is to discover what animal and plant species were available to be exploited and, in the case of hominids, what cultural adaptations made such exploitation possible. Short time-base parochial studies are considered most desirable in this context.

Palaeoanthropology (the study of fossil primates) involves all three of these aims. Throughout most of the primate fossil record, species and evolutionary lineages are studied not only with regard to their lifestyles, but also with respect to the communities with which they are associated. During the later

Pleistocene record for fossil hominids the special case of palaeobiology comes into operation as the study of prehistoric economies. Generally speaking, it is unrealistic to expect detailed results similar to those expected of modern ecological studies. Reconstructions are hypotheses that must be tested which is not to say that palaeoecology cannot acheive useful results, but it is important to be aware that since direct observation is impossible even the best reconstructions are completely conjectural. While it is important not to throw the baby out with the bath water, it is equally important to realise that there is an enormous amount of dirty bathwater to be disposed of. The task attempted in this research is the disposal of bathwater and the realistic appraisal of the capabilities of the baby.

e. What Palaeoecological Methods are Available?

The evolutionary relationships with which palaeoecologists are concerned tend, in one sense or another, to be adaptive in nature. This adaptation can be regarded as occurring at three levels each of which is associated with a particular approach to palaeoecological reconstructions:

i. The level of the individual organism (indicator species methods).

ii. The level of groups of individuals (population methods).

iii. The level of groups of groups or populations (community diversity methods).

An alternative way of dividing palaeoecological approaches is through the method of inference used: Whether conclusions are reached by inference from taxonomic identity or inference from adaptive structures. Indicator methods are those where species (taken either individually or as groups) are regarded as being diagnostic of particular environmental conditions. Diversity methods are those where adaptive patterns shown by ecologically defined groups of species are regarded as an important guide to the prevailing conditions (patterns such as relative abundance of species and ecological structure of a community). The distinctions between these two approaches and the consequences of the different methods of inference are discussed in chapter 2.

## 2. Introduction to the Thesis.

### a. Aims and Scope of the Research.

It was decided at the outset that it would be impractical to examine all palaeoecological methods in depth. Therefore only a limited number of the methods available will be described in detail. The examination will be restricted to those methods that do not require detailed quantitative data, i.e. those that can be used with the kind of presence/absence data that can be obtained from faunal lists alone. This eliminates some

of the indicator species methods, all the population methods, and some of the community diversity methods. A brief outline of most of these methods will be given below, but only a selected few will be examined in detail and applied in the case studies.

b. Thesis Layout.

The thesis is divided into two sections, the first dealing with theoretical issues, the second with the practical application of some of the methods discussed in the first section. Section I consists of the Introduction (chapter 1) and chapters 2 to 5. Chapter 2 deals with neoecological concepts that relate to the palaeoecological methods described later. These concepts are mainly concerned with the distribution of species in time and space with respect to habitats or other species. Chapter 2 concentrates on two issues: Firstly, niche theory and the explanation of distribution patterns, and secondly, the measurement of certain characteristics of these patterns.

Chapter 3 outlines three palaeoecological approaches to the problems of environmental reconstruction and explores their theoretical backgrounds. All the most important palaeoecological methods that have been applied to the mammalian fossil record are discussed in this chapter and they are compared and contrasted in terms of their relationship

to modern ecological concepts, the data they require, the conditions that must be satisfied for their successful use and the results they are likely to produce.

Chapter 4 describes some of the most important modern habitat types and analyses communities from these habitats using the methods developed and described in the previous chapter. This is necessary for several reasons: Although many of the constraints on the various methods can be arrived at theoretically, the practical limitations can only be discovered by applying the methods to the best data available, which in this case are those for modern species and communities. Once it has been determined that the methods can be made to work, they then have to be "calibrated" to discover the patterns corresponding to different habitats and also the levels of discrimination that can be achieved.

The final chapter in the first section, chapter 5, illustrates the influence on some palaeoecological methods, of the kinds of taphonomic bias that commonly affect the fossil record. A series of simulations are presented which involve the controlled removal of species from modern communities originating from known habitats. These simulations show the sensitivity of different methods to various degrees of species loss, and the results obtained form an important basis for the interpretation of fossil faunas.

Section II deals with the practical application of the methods described in section I. Two major areas of study, the European Pleistocene and the African early Miocene, have been chosen to illustrate the strengths and weaknesses of various palaeoecological methods.

Chapter 6 describes case studies of two sites from the Pleistocene of Europe. The faunas recovered from these sites are analysed using many of the palaeoecological methods discussed in section I. These case studies highlight a number of problems, most notably that of dealing with habitats not represented in the modern sample. Europe experienced dramatic climatic fluctuations during the Pleistocene and some habitats of the past are unlike any of those known at present. Chapter 7 concentrates on this problem of extinct habitats. A large number of Pleistocene faunas from Europe and Western Asia are analysed and evidence of several non-extant habitat types is identified at a number of sites.

Chapter 8 deals with a series of sites of early Miocene age from Africa, nearly all of which are associated with fossil hominoids. Some of the strengths of diversity methods for examining community structure are demonstrated by this case study, and some important conclusions are drawn concerning the evolution of the monkeys and the apes, and changes in the structure of African tropical forest communities.

The final chapter, chapter 9, concludes the thesis by drawing together the theoretical aspects of palaeoecology discussed in the first section and the practical applications of some palaeoecological methods demonstrated in the second section. Final conclusions are reached about the way in which palaeoecology should be used, and the kinds of results it can achieve.

Chapter 1: Summary.

Chapter 1 provides an introduction to the subject matter and the layout of the thesis. The thesis is intended to do two things, firstly, to examine and compare the theoretical merits of a number of palaeoecological methods, and secondly, to illustrate how these methods can be used in practice to analyse fossil faunas.

The relationship between neo-ecology and palaeoecology is discussed and it is seen that palaeoecology relies on a strong theoretical foundation in modern ecological concepts. It is also seen that the importance of palaeoecology lies in its ability to provide the necessary contextual evidence against which to set studies of faunal and community history, the evolution of biological lineages, palaeobiology and lifestyle reconstructions.

These points serve as a basis for the in-depth exploration of several issues such as the relationship between neo-ecology and palaeoecology, the comparison of different palaeoecological methods and the mean of using these methods in practice, which is found in the main body of the thesis.

The structure of the thesis is also outlined: Theoretical issues are dealt with in chapters 2 to 5 and the practical use of various methods are illustrated in chapters 6 to 8. Chapter 9 concludes the thesis.

# Chapter 2

## Modern ecological concepts relating to the distribution of species

## 1. Introduction.

All the palaeoecological methods described below rely on the fact that species and communities are distributed non-randomly with respect to environmental conditions. The area in which modern ecology can contribute most to the understanding of palaeoecology is in the study of species distribution. The distribution of species and the assemblage of communities is most easily discussed in terms of the ecological niche, which was considered by Grinnell (1917) to be "the ultimate distributional unit". Although the niche concept has been considerably modified since the time when Grinnell was writing, it can still be seen as the most convenient way of analysing the distribution of species. In this chapter, specializations at various adaptive levels, ranging from that of the individual to that of the community, are discussed and related to Niche Theory in order to provide the basic theoretical foundation underlying the palaeoecological methods described in chapter 3.

## 2. The Niche Concept.

The concept of the niche has appeared in a number of forms and as well as expressing information about the distribution of species populations with respect to environmental variables of many kinds (both

biotic and abiotic), it also allows the adaptations shown by different species to be compared in a more abstract way. There are three ways in which the term is most commonly used:

i. Spatial or habitat niche.

ii. Trophic niche.

iii. Multidimensional or hypervolume niche.

The meaning of the term has changed through time. It originated with Grinnell (1917; 1928) who considered the niche to be "the ultimate distributional unit within which each species is held by its structural and instinctive limitations". This concept was developed with the principal purpose of analysing the distribution of species in relation to physical habitats and thus entails the concept of the spatial or habitat niche.

The ideas proposed by Elton (1927) are quite different. He considered that the niche represented the functional position of an organism in its community and this idea of the niche as a description of the species' functional status in relation to other species is now very widely accepted. Elton concentrated on the exploitation of food resources and although his definition leads directly to the idea of the trophic niche, the concept is easily extended to include other limiting resources.

The definition proposed by Hutchinson in 1956 is more inclusive still and more abstract in form. Hutchinson regarded the niche as a multidimensional space or hypervolume within which the environment permits a single species to survive indefinitely (Hutchinson, 1956). Environmental variables define axes which outline the dimensions of an abstract multidimensional space called niche space. Every species can adapt to, or tolerate, some range of each variable, and for each species, the upper and lower tolerance limits on each axis define that part of the total available niche space that the species is able to occupy. Hutchinson termed this bounded hypervolume the "fundamental niche" (Hutchinson, 1958; 1965; 1967). A real species population lives within the influence of other species in the community and under these conditions a reduced hypervolume known as the "realised niche" is usually occupied. It follows that the whole of the realised niche must fall within the boundaries of the fundamental niche. In short, the fundamental niche is an expression of the conditions that a species can tolerate when not constrained by competition or other biotic factors, whereas the realised niche is a smaller hypervolume and is the part of the fundamental niche occupied by a real species population under the influence of non-limiting, density-dependent, biotic and abiotic constraints.

The hypervolume niche is the most inclusive sense in which the term is currently used. It takes account of the physical space occupied by a species (incorporating Grinnell's concept) and the functional status of the organism in a real community (Elton's concept of the niche). One of the main advantages of the hypervolume niche is that it is (at least in principle) amenable to mathematical manipulation. A second advantage is that the concept treats spatially extensive habitat factors and intensive intracommunity factors within a single framework.

An important position is held by the work of Gause (1934) due to the fact that in practice the niche concept is intimately involved with the competitive exclusion principle. Competition is considered to be one of the factors primarily responsible for structure in communities (Odum, 1971; Whittaker, 1970). It is considered that two direct competitors (i.e. two species occupying identical niches or showing a large amount of niche overlap) cannot coexist indefinitely in the same community, and eventually one will displace the other. Species can only coexist if they are non-competitive and the selective disadvantage of competition can result in diversification. In the short term this may occur as character displacement (Gause, 1934; Odum, 1971), while in the long term, evolutionary processes lead to diversification and the scattering of species populations in niche space.

The more abstract and complex ideas of niche theory can hardly be applied directly to palaeoecology in the form described above. Niche Theory belongs to neoecology but the ideas that it entails can be translated into terms that palaeoecologists can understand by substituting the term "habitat" for "environmental conditions" and by considering that the limits of a species tolerances to environmental variables can be defined by its adaptations. These synonomies are not as far fetched as it might at first appear. "Habitat" is a term that refers to a set of commonly associated environmental conditions and characteristics. Similar habitats are generally the result of similar environmental conditions. Likewise, the conditions which a species is able to tolerate or survive are usually determined by its adaptations. Bearing these considerations in mind, it is most convenient to discuss the consequences of Niche Theory for palaeoecology at three levels of adaptation:

i. Adaptation at the level of individuals.
ii. Adaptation at the level of groups of individuals.
iii. Adaptation at the level of communities.

This division is purely heuristic and should not be taken to mean that specializations aid the survival only of the individual or of the group. The two aims are indivisible and distinction is made for the sake of convenience merely because there are certain adaptations

that are observed in individuals of a species and other adaptations that can only be observed in groups of individuals.

3. Adaptations at the Level of the Individual.

Provided that a species is not precluded by its absence from the biota of the region or by the chance effects of historical accident, the question of whether or not it is found in a given habitat is one that can be analysed in terms of Niche Theory. The environmental conditions associated with the habitat define the total niche space that is available, and the presence of the species depends in the first place on whether its fundamental niche can be supported in this niche space, and secondly whether the presence of this niche is prevented by the density-dependent factors which arise as a result of the presence of other species in the community. The second factor concerns the assemblage of communities and will be dealt with in another part of this chapter. The first factor is related to the adaptations shown by a species which will be discussed further here.

The fundamental niche of a species is defined by the limits of its tolerance of a multitude of environmental variables. In practice these limits are set by the species' adaptations. Specializations that

can be observed at the level of the individual include all adaptive characteristics that are found in any normal individual of the species. Adaptive characters are those which promote the fitness and the survival of the species. Characters that do not affect fitness are considered to be non-adaptive. The kinds of adaptations that are commonly observed in individuals can be either morphological or behavioural and information about the feeding, digestive, reproductive, locomotor and sensory systems, among others, can contribute a considerable amount to knowledge about the species' fundamental niche. A species whose tolerances are narrow is usually regarded as being specialized, whereas a species having wide tolerances is regarded as being adaptable and generalized.

Generalized adaptations are not particularly useful for palaeoecology, but specialized patterns which suggest narrow tolerances can be interpreted as indicating that the species was adapted to a limited range of conditions and was perhaps found only in a limited range of habitats. Palaeoecology is further constrained by the fact that behaviour cannot be fossilized, at least not directly, and in the absence of the behaviour patterns that make morphology functional, the only evidence that is available about adaptive specializations is based on morphological characters.

## 4. Adaptations at the Level of the Group.

Group adaptations must also be considered because species are not distributed as isolated individuals but as members of groups, populations and demes. A species population must be able to survive the prevailing conditions within an area for that area to form part of the species' distribution range. Specializations at the group level largely concern group behaviour, social organisation, population parameters and life-history phenomena that aid a population's fitness and survival. Unlike individual adaptations, these can only be observed operating in the context of a group or population. For instance, Clutton Brock and Harvey (1977) studied the distribution of various behavioural adaptations operating at the group level among extant primates. They showed that characters such as group biomass, home range size, population density, day range, sexual dimorphism, feeding group size and biomass, and socionomic sex ratio may all have an adaptive role to play in promoting the survival of the group, individuals within the group and hence the survival of the species as a whole. Studies of this kind have been carried out on several mammal groups, for instance, Primates (Clutton Brock & Harvey, 1976; 1977; Crook, 1972; Crook & Gartlan, 1966; DeVore, 1963; Kummer, 1967; Struhsaker, 1969; Aldrich Blake, 1970; Eisenberg *et al.*, 1972; Goss Custard *et al.*, 1972)

Carnivores (Bertram, 1973; 1976; Kruuk, 1972; Wilson, 1975) and ungulates (Jarman, 1974; Wilson, 1975) and also among colonial microorganisms, invertebrates, social insects, cold-blooded vertebrates and birds (see Wilson, 1975; and references cited there).

## 5. Adaptations at the Level of the Community.

A biotic community is an assemblage of populations living in a prescribed area or physical habitat (Whittaker, 1970). Species are not normally distributed as isolated populations and a habitat usually contains a number of sympatric species populations each with it own set of tolerances and adaptations and each exploiting a different part of the environment. The community is often regarded as an organised unit to the extent that it has characteristics which are additional to those of its component individuals and populations. One of these characteristics is "diversity". Throughout this thesis the term diversity refers to within-habitat diversity, that is, the diversity of a community belonging to just one habitat, not that found in a sample drawn from a series of habitats. Cody (1975), following a suggestion by MacArthur (1965), has made use of the important distinction between what he calls "alpha-diversity" and "beta-diversity". Alpha-diversity is within-habitat diversity whereas beta-diversity is a

measure of species replacement rates or cross-habitat diversity measured along a habitat gradient. It is clear that the factors controlling alpha and beta diversities are likely to be different and that it is important not to confuse the two (see for instance Gingerich et al., 1980; and Andrews, 1982).

A brief review of the literature makes it clear that the term "species diversity" has been used in a number of different senses each of which has a different mathematical connotation as well. Foremost among the meanings of species diversity are:

i. Species richness.

ii. Heterogeneity.

iii. Equitability.

i. Species richness refers simply to the number of species in the community. It is probably the most frequently encountered and certainly the most easily measured form of species diversity. It suffers the disadvantage that all species are ranked equally, irrespective of their commonness or importance and for this reason species richness conveys comparatively little information about the community.

ii. Heterogeneity is a form of species diversity that combines the number of species with some measure of their relative importances such as biomass, population

productivity or relative abundance. The commonest ways of measuring heterogeneity mathematically are the Shannon-Weiner and Brillouin information functions. These are derived from information theory and both have a number of properties that make them particularly suitable for quantifying heterogeneity in ecological communities (Pielou, 1966; 1977:293). When the Shannon-Weiner function is used, heterogeneity (H') is given by the expression :

$$H' = -\sum_{i}^{s} p_i \ln p_i \qquad (2.1)$$

(where s = the number of species in the community;
$N_i$ = the number of individuals in the ith species;
N = the total number of individuals in the sample;
and $\sum_{i}^{s} N_i = N$; $p_i = \frac{N_i}{N}$ ; $\sum_{i}^{s} p_i = 1.$)

This expression measures the uncertainty that a randomly sampled individual will belong to a particular species in the community. Thus, as the number of species increases and as the species in a community become more equal in importance or abundance, it becomes increasingly uncertain to which particular species a randomly selected individual will belong (Pielou, 1977).

The Shannon-Weiner function is strictly defined in information theory to apply only to an effectively infinite "population", that is, a population which is too large to be completely censused. Under these conditions H' provides only an estimate of heterogeneity

based on a sample drawn from the community (Pielou, 1966). In the event that the community can be completely censused, heterogeneity can actually be measured without error using the Brillouin function, (Pielou, 1977):

$$H = (1/N)\ (\log N! - \sum^{s} \log N_i\ ) \qquad (2.2)$$

(Where s, N and N are as above.)

It should be noted that there is a mathematical similarity between the Brillouin and Shannon-Weiner functions and as $\min.N_i \to \infty$ ; $H \to H'$.

Pielou (1966; 1975; 1977) provides an extensive discussion of the derivation, theory and practical applications of the mathematical aspects of heterogeneity and species diversity.

iii. Equitability is an expression of the evenness with which the species of a community are represented in terms of the chosen importance measure. The number of species in the community is not taken into account. The value of H' (equation 2.1) reaches a maximum when all species are equally abundant or important and under these conditions H' depends on the number of species alone and for the Shannon-Weiner function the maximum value of H' (H'max) is given by:

$$H'max = \ln S \qquad (2.3)$$

(where S= the number of species in the community.)

The equitabilty (H'') of the species in a community can

be estimated by the following expression:

$$H'' = H'/H'max. \qquad (2.4)$$

H'' has a maximum value of 1 which is reached when all species are equally common and H' = H'max.

It is fashionable in ecology to regard the community as an integrated system whose structure is governed by internal interactions, although the community can equally be regarded as the epiphenomenal result of overlapping species distributions (Hofmann, 1979). There is considerable debate over this question, which is as yet still largely unresolved, at least in the detail necessary to allow the concepts to be distilled into theoretical palaeoecology. At present, the problem of what factors control community structure does not need to be solved, since even epiphenomenal communities can be regarded as possessing structure and diversity, and a sufficiently firm foundation is provided by the empirical observation that certain regularities can be found in the relationship between community structure and habitat. However, it will be possible to achieve more detailed palaeoenvironmental reconstructions once the control of community structures is more fully understood. The main structure controlling factors have been highlighted by a number of theories proposed to explain the gross differences between communities from different areas.

It has been known at least since the time of Charles Darwin and Alfred Wallace that communities in the tropics contain many more species than those in temperate regions, and that these species also tend to be more varied in their adaptations. This fact was highlighted by G.E. Hutchinson in 1959 and since then the effects of latitude and environment on the number of species to be found in an area have been well documented for many animal groups, for instance in birds (Karr, 1971; Karr & Roth, 1971; MacArthur, 1969; MacArthur et al., 1966; Orians, 1969; Cody, 1966; 1975; Diamond, 1973; Recher, 1969), rocky intertidal communities (Paine, 1966; Dayton, 1971), lizards (Pianka, 1966; 1967; 1975), and mammals (Simpson, 1964; Brown, 1975; Fleming, 1973).

Differences in species richness are usually regarded as the result of variation in either the size of niches (hypotheses about environmental stability, time-stability, competition and predation) or in the amount of niche space available (hypotheses concerning spatial heterogeneity and productivity), although the role played by chance factors (habitat size and isolation) should not be forgotten. Probably no single hypothesis is sufficient on its own and in practice several factors will be found to exert an influence on the number of species in a habitat.

Environmental Stability.

This hypothesis states that the more stable the environment the greater the species diversity. This may be for one of two reasons: Either because regions of greater stability allow the evolution of greater specialization which results in smaller niches and the packing of more species into the niche space available in the habitat, or because stable environments do not exert such rigorous selection so that species are less likely to become extinct in stable areas.

Time-stability.

This explanation relies on two lines of thought. Firstly, biotas in the tropics are likely to evolve and diversify more rapidly than those in the temperate and polar regions. Secondly, diversity is a product of evolution and will therefore depend on the length of time through which the biota has developed uninterrupted by climatic disasters like glaciations which do not occur in the tropics. All communities diversify in time but older communities, which have more species than younger communities, occur in more constantly favorable climates.

Competition.

It has been suggested that diversity in temperate and polar regions is controlled by physical factors in the environment which exert strong selective

influences. In the tropics where the physical environment is less rigorous, biological competition is the major controlling factor. Keener competition results in smaller niches and the packing of more species into a given habitat. Smaller niches are manifested in the form of specializations and more restricted habitat requirements. Such an argument obviously relies on some kind of competitive exclusion, whether or not increased diversity is the result of narrower niches or increased niche overlap. Competition clearly plays a role in community organization in as much as a species may be competitively excluded from an otherwise suitable habitat (see for instance Brown, 1971) but it is impossible to tell to what extent it can be used to explain diversity gradients.

Predation.

Paine (1966) believes that predation can control prey species in such a way that competition between them is reduced, dominance becomes less effective and species richness is maintained at a higher level than would be the case in the absence of predators. Thus in the tropics larger numbers of predators hold prey populations down to levels that reduce competition sufficiently to allow the addition of more prey species with a resultant increase in richness. The suggestion has been illustrated using invertebrates from the intertidal zone of a rocky shore (Paine, 1966).

Spatial Heterogeneity.

This factor can operate on a macro- or a micro-level. Topographic (macrospatial) relief certainly has a marked effect on beta diversity, mainly because regions of high relief contain many habitats in a small area (Simpson, 1964). Microspatial heterogeneity refers to complexity due to "organism-sized" objects on a local scale and has been regarded as a key determinant of species diversity in several groups, for instance, birds (MacArthur & MacArthur, 1961; MacArthur, 1964; MacArthur et al., 1966; Recher, 1969; Karr & Roth, 1971), fish (Sheldon, 1968), and lizards (Pianka, 1966; 1967). The argument is that there is an increase in environmental complexity from the poles to the tropics. Physical complexity in a habitat allows species to avoid competition by spatial segregation so that the more complex the physical environment the more complex the communities that occupy it and the higher the species richness.

Productivity.

Connell and Orias (1964) proposed that greater productivity would result in greater species richness. Pianka (1967) concludes that length of growing season and warm season productivity are both factors which affect the diversity of lizard species in North American flatland deserts. The productivity of the habitat sets an upper limit to the biomass of primary consumers that

can be supported. The effective upper limit is set by the least productive part of the year and thus the relation between productivity and diversity depends on how primary productivity is spread throughout the year.

Habitat size.

MacArthur and Wilson, in their monograph on the theory of island biogeography (1967), coined the concept of the species-area curve to explain some of the differences in species richness that occur between islands in areas of relatively uniform climate. This concept can be extended to apply to isolated "islands" of a habitat. A population needs a certain minimum number of mature individuals in order to constitute a viable breeding population. The size of a habitat "island" will limit the size of a species population and, as the minimum viable population size is approached, the probability of the population becoming extinct increases. When this is averaged over several species populations, small areas of habitat will tend to have fewer species than large areas of the same habitat type.

Habitat isolation.

Islands generally recruit species by colonization from donor or source areas. The theory of island biogeography predicts that the chances of an island being colonised bear an inverse relationship to

its distance from the source area. Overall, the number of species to be found on an island will become less with increasing distance. Habitat islands can be isolated by geographical barriers such as rivers and mountain chains, and also by areas of a different habitat type. Isolation will affect the species richness of a habitat in a way similar to that predicted by the theory of island biogeograhy (MacArthur & Wilson, 1967) so that increased isolation results in decreased species richness. This effect has been documented for birds in Peru by Terborgh and Weske (1969).

Chapter 2: Summary.

Chapter 2 outlines modern ecological concepts relating to the distribution of species which provide the theoretical foundations of palaeoecological methods. Palaeoecological methods rely on the fact that species are distributed non-randomly with respect to environmental conditions, thus the area in which neo-ecology can contribute most to the understanding of palaeoecological methods is in the study of distributions.

Species distributions are most easily studied in terms of the ecological niche. The concept of the niche is discussed and related to adaptive specializations that can be observed at the level of the individual, population and community. The specializations that can be observed at the level of the individual are morphological and behavioural adaptive characters found in any normal individual of a species. Group adaptations concern factors such as social organization, population parameters and life-history phenomena, which are normally expressed behaviourally, although there may be morphological correlates.

Populations live together in communities, one of whose characteristics is diversity. This is a term that has been used in several ways in the past, ranging from the number of species to measurements of the relative importance of the species in the community. The mathematical expressions of these meanings are described and a number of factors responsible for structure in communities are discussed. These factors can be used to explain the differences between communities from different environments in terms of differences in size of niches or the total amount of niche space available, or in terms of chance historical factors.

# Chapter 3

## Palaeoecological methods

## 1. Introduction.

In chapter 1 a very brief outline was given of the palaeoecological approaches currently in use, and the way in which they correspond to levels of adaptation from that of the individual, through that of the group or species population, to that of the community. The way in which these levels relate to modern ecological concepts was discussed in chapter 2. In this chapter some palaeoecological methods will be examined in greater detail and contrasted in terms of their differing approaches to the problems of environmental reconstruction. The methods will be discussed in the following order:

i. Indicator species methods.

ii. Population methods.

iii. Community diversity methods.

Frequently, the only information that is available about a fossil fauna is a list of the species it contains. Methods which cannot be applied to the simple presence/absence data provided by faunal lists are not discussed in detail. This includes the population methods which require good quantitative information about traits such as sexual dimorphism, sex ratio and age-structure of the population, and some of the indicator and diversity methods which require details of minimum number of individuals and relative abundance of species in the fauna.

The concepts of fundamental and realised niches as they were described above provide one way of dividing palaeoecological methods on theoretical grounds.
The fundamental niche describes the conditions that the species is able to survive through possession of certain adaptive specializations which can be observed either at the level of individual members of a species, or at the level of groups of individuals. Indicator methods concentrate on the specializations of individual species and thus relate largely to the fundamental niche.
The realised niche describes the specific conditions occupied by a species population as part of a given community at a given time. Realised niches can thus only be observed in the presence of the density dependent effects exerted by other species populations and any method focusing on the realised niche must work at the level of the community. Consequently, diversity methods, which concentrate on the structure and other characteristics of communities, relate primarily to the realised niche.

Unfortunately modern techniques cannot be used directly as palaeoecological methods for a number of reasons, most of which can be traced to a common cause; the fact that the data presented by the fossil record do not contain a great deal of information. The result is that palaeoecologists are forced to make assumptions about fossil species and communities that would never

be acceptable in the context of a neoecological study. The data available are certainly not adequate to allow analysis in terms of fundamental and realised niches, and although a theoretical connection is implied in the approaches adopted by the various palaeoecological methods, the data are too poor for concepts such as these to be directly useful. Furthermore, modern patterns are not well understood and knowledge about the controls on extant species and communities is extremely patchy. For instance, it is known that species tend to be associated with particular conditions because of their adaptive specializations, and that in some cases the presence of a species can be taken to indicate the existence of certain environmental conditions. This is the basis of indicator species methods, however, precise details of the environmental factors concerned are known for very few living species. Similarly, insufficient is known about the factors controlling community structure to make any but the most superficial kind of analysis appropriate. The main justification of the diversity methods is the empirical observation that communities from similar habitats have similar structures, while those originating from different habitats have different structures. Unfortunately, too little is known of the factors determining community structure even to allow an accurate assessment of how well the assumption of ecological uniformitarianism holds good.

## 2. Indicator Methods.

Indicator methods work by allocating habitat preferences to species in the fossil record and then using the occurrence of those species in a fossil fauna as a means of identifying the habitat of the fauna. The main problem that has to be overcome is that the behaviour of species in the fossil record cannot be observed directly and the habitat preferences of these species are completely unknown. This information has to be inferred from other sources of evidence, for instance from the preferences of the closest living relatives of the fossil species or from clear-cut patterns of functional morphology. For an indicator method to work satisfactorily it is necessary to identify the fossil species and its living relatives, to be able to assess the closeness of this relationship, and to take into account the variability displayed in the habitat preferences of many living species. Considerable importance thus falls on phylogenetic interpretations and knowledge about the habits of living species. There are several variations on this basic theme which can be divided into three groups:

a. Traditional indicator methods.

b. Methods weighting variability.

c. Methods using microhabitat associations.

a. Traditional Indicator Methods.

In the traditional sense an indicator species is a species that is considered to have a well defined habitat preference, and its occurrence in a fossil fauna is held to indicate the presence of that habitat type. Until recently, traditional indicator methods were virtually the only palaeoecological technique in common use. They can usually be distinguished by two features, firstly that species are regarded as having an invariable preference for a single habitat type, and secondly, that the presence of just one or two characteristic species is often sufficient to allow the habitat of the whole fauna to be determined. Where several species consistently occur together they may be considered as being a significant ecological unit in their own right and used as an indicator group. This latter technique has been used for South African Pleistocene and Holocene sites using large mammals (Klein, 1980) and small mammals (Avery, 1982). In some cases the abundance of one indicator species relative to another has been used as a means of determining the habitat of a fossil fauna, although this often seems to have been a reaction to the presence of two indicator species traditionally associated with quite different habitats: Where two species give conflicting indications, relative abundance is invoked to show which is the more important member of the fauna and therefore likely to give the most reliable indications.

For instance, de Lumley (1969) bases many of his biostratigraphic and palaeoecological conclusions for faunas spanning the interval from the Riss to the Wurm glaciations on the relative abundance of Cervus elaphus (a forest dweller) compared with that of Equus species (prairie dwellers) in conjunction with the presence of one or two other species such as Capra ibex, Rangifer tarandus and Sus scrofa. Similar approaches have been adopted for middle-eastern faunas by Tchernov (1968) and Bate (1937). Traditional indicator methods in general can be criticised on a number of points, for instance:

> The traditional methods are naive in the assumption that species have an invariable preference for a single habitat type. A species' niche fills only part of the total niche space available, thus a species does not adapt to the whole habitat but only to a part which is often called its microhabitat or biotope. Only a species associated with a microhabitat that is found in a restricted range of habitats has a habitat preference that is sufficiently narrow to make it a useful indicator in traditional terms.
>
> The less closely related a fossil form is to modern species the more uncertain its allocated preferences must be. In practice this means that indicator methods become less reliable with faunas of

increasing age. Despite this, very little attempt is made in the use of traditional methods to allow for the effects of variability in the closeness of phylogenetic relationships.

The whole fauna is rarely used and conclusions are often drawn from a mere handful of species. Thus, despite the fact that an enormous amount of information is lost during fossilization, still more is voluntarily discarded when only a few species are considered. Quantitative data are rarely used except as an ad hoc measure where clear-cut results are not forthcoming even though information such as relative abundance can be readily incorporated into any method that allows the contributions of individual species to be weighted.

Since the habitats of fossil indicators are inferred from the habits of living species, the preferences of fossil species are defined in terms of modern habitats alone. This means that only modern habitats can be identified in the fossil record, and as far as traditional methods are concerned "extinct" habitat types do not exist.

Further specific criticisms of the way traditional indicators have been used to analyse European faunas of Pleistocene age are discussed in chapter 7.

b. Methods Weighting Variability.

Although indicator methods have been in use for a long time, it is only recently that some better methods have been introduced which attempt to overcome some of the problems outlined above by taking a more realistic approach to variability in phylogenetic relationships and habitat preference:

i. Habitat Spectra (HS).

The method used for constructing Habitat Spectra was first described by Van Couvering (1980). In forming a Habitat Spectrum each species of a fauna is given a habitat range across a series of recognised habitat types based on the present range of its closest living relative, its morphology, and well documented associations of the species in the fossil record. This range is weighted according to the closeness of relationship to modern relatives (6 if the species itself is still living, 5 if the genus is extant, 4 for the tribe, 3 for the subfamily, 2 for the family and 1 for any higher category). The Habitat Spectrum is constructed by adding together, for each habitat type, the respective weightings for all species whose range includes that habitat. If the total of weightings for one habitat type is dominant, this is taken to be the habitat of the fauna. Advantages of this method are: that the whole fauna is used; each species is given a habitat range which is a more realistic representation

Table 3.1.

The table shows the Habitat Spectrum weightings for the species comprising a hypothetical boreal forest mammal community. The sums of all weightings for each habitat are shown in the totals at i. The weightings in brackets are those where the corresponding Taxonomic Habitat Index weighting is less than 0·1 (see p. 76). The adjusted totals (which do not include the figures in brackets) are given at ii.

The Habitat Spectrum patterns corresponding to each of the two sets of totals are shown in figure 3.1 (p. 69). A key to the column headings is given in the caption to figure 3.1 (p. 68) and in appendix 5 (p. 699).

Table 3.1. Habitat Spectrum weightings for a hypothetical boreal forest community.

| Taxon | | Habitat | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Tu | B | D | M | S | Fs | A | T | Mo |
| Erinaceus europaeus | | - | - | 6 | 6 | 6 | 6 | - | - | 6 |
| Sorex minutus | | 6 | 6 | 6 | (6) | - | - | - | - | (6) |
| Sorex araneus | | 6 | 6 | 6 | 6 | - | 6 | - | - | 6 |
| Sorex sp. | | (5) | 5 | 5 | (5) | (5) | (5) | 5 | - | (5) |
| Soricidae | | (2) | 2 | 2 | (2) | (2) | (2) | 2 | (2) | 2 |
| Neomys fodiens | | 6 | 6 | 6 | - | - | 6 | - | - | 6 |
| Talpa europaea | | - | 6 | 6 | 6 | 6 | 6 | - | - | - |
| Lepus timidus | | 6 | 6 | (6) | - | - | (6) | - | - | 6 |
| Lepus sp. | | (5) | 5 | 5 | (5) | 5 | (5) | 5 | 5 | 5 |
| Sciurus vulgaris | | - | 6 | 6 | 6 | - | 6 | - | - | - |
| Pteromys volans | | - | 6 | 6 | - | 6 | - | - | - | - |
| Myopus schisticolor | | 6 | 6 | - | - | - | - | - | - | (6) |
| Clethrionomys rutilus | | 6 | 6 | - | - | (6) | 6 | - | - | - |
| Clethrionomys sp. | | (5) | 5 | 5 | - | (5) | (5) | - | - | 5 |
| Arvicola terrestris | | 6 | 6 | 6 | (6) | 6 | 6 | - | - | (6) |
| Ondatra zibethicus | | - | 6 | 6 | - | 6 | 6 | - | - | - |
| Microtus agrestis | | (6) | 6 | 6 | (6) | - | - | - | - | - |
| Microtus oeconomus | | - | (6) | - | - | - | 6 | - | - | 6 |
| Microtus sp. | | (5) | 5 | 5 | (5) | 5 | (5) | 5 | (5) | 5 |
| Micromys minutus | | - | 6 | 6 | (6) | 6 | 6 | - | - | - |
| Apodemus sylvaticus | | - | - | 6 | 6 | 6 | 6 | 6 | - | - |
| Apodemus sp. | | - | (5) | 5 | 5 | 5 | (5) | (5) | 5 | 5 |
| Muridae | | - | (2) | 2 | 2 | 2 | (2) | 2 | (2) | 2 |
| Sicista betulina | | - | 6 | - | - | 6 | 6 | - | - | - |
| Canis lupus | | 6 | 6 | 6 | 6 | 6 | 6 | (6) | - | (6) |
| Vulpes sp. | | (5) | (5) | (5) | (5) | 5 | (5) | 5 | (5) | (5) |
| Nyctereutes procyonoides | | - | 6 | 6 | - | 6 | - | 6 | - | - |
| Gulo gulo | | 6 | 6 | - | - | 6 | - | - | - | 6 |
| Mustela erminea | | 6 | 6 | 6 | - | 6 | 6 | 6 | - | 6 |
| Mustela nivalis | | 6 | 6 | 6 | 6 | 6 | 6 | (6) | - | (6) |
| Mustela sp. | | (5) | 5 | 5 | (5) | 5 | (5) | (5) | - | 5 |
| Martes martes | | - | 6 | 6 | 6 | - | - | - | - | 6 |
| Meles meles | | - | 6 | 6 | 6 | 6 | 6 | 6 | (6) | (6) |
| Alces alces | | 6 | 6 | - | - | - | - | - | - | 6 |
| Totals | i | 116 | 172 | 151 | 118 | 123 | 141 | 60 | 30 | 129 |
| | ii | 78 | 160 | 140 | 67 | 105 | 96 | 48 | 10 | 83 |

Figure 3.1.

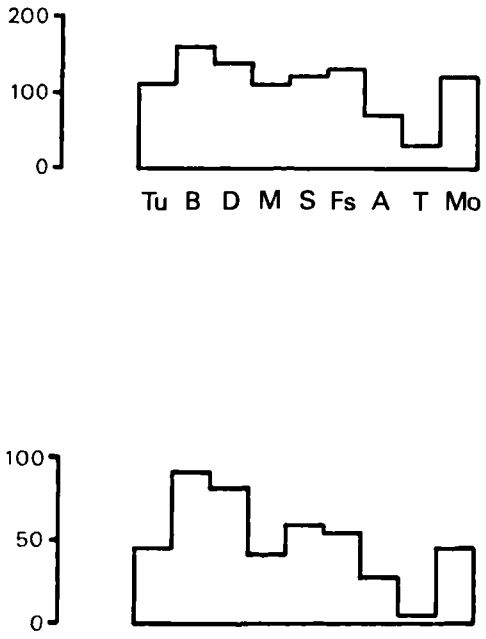
This figure shows the Habitat Spectrum patterns for the community listed in table 3.1. The upper figure uses the details shown at i in table 3.1, based on all weightings for all species. The lower figure uses the totals shown at ii, which are those obtained after the exclusion of Habitat Spectrum weightings for each species in any habitat where the equivalent Taxonomic Habitat Index weighting is less than 0·1 (see table 3.2). It can be seen that the lower figure gives a slightly better indication of the habitat occupied by the community, but this figure should also be compared with the pattern shown in figure 3.2, which results from the analysis of the same community using Taxonomic Habitat Index.

Key:

| | |
|---|---|
| Tu | Tundra |
| B | Boreal forest |
| D | Deciduous forest |
| M | Mediterranean habitats |
| S | Steppe |
| Fs | Forest-steppe |
| A | Arid steppe/semidesert/desert |
| T | Tropical |
| Mo | Montane |

(Note: A fold out key to all Habitat Spectra, Taxonomic Habitat Index and Residual Diversity patterns is given at Appendix 5.)

Figure 3.1. Habitat spectrum of a boreal forest community.



of the way modern species behave; proper significance is given to species that are truly restricted to a narrow range of habitats; the closeness of relationship between modern and fossil forms is weighted to allow for the error involved in allocating habitat preferences of distantly related species; relative abundance data can also be incorporated into this method.

The method is illustrated in table 3.1 and figure 3.1 which show the species weightings and resulting Habitat Spectrum for a hypothetical community based on a European boreal forest community.

ii. Taxonomic Habitat Index (THI).

Although this method was developed at the same time and by the same authors as ecological diversity, details have only recently been published (Nesbit Evans et al., 1981). The Taxonomic Habitat Index takes into account the ecological variability of groups at different taxonomic levels. Each species of the extant African mammal fauna had its preferences for a series of habitat types weighted according to the frequency with which it is to be found in each habitat. Thus a species occurring only in forest would be given a weighting of 1.0 for forest and 0 for all other habitats, while a species that occurs equally in forest, woodland, and bushland would be weighted 0.33 for forest, 0.33 for woodland, 0.33 for bushland and 0 for all other habitats.

Each species in a fossil fauna is then given a weighting for each of the recognised habitat types according to the averaged habitat weightings of all the living species contained within the lowest taxonomic level at which the fossil species is related to its closest living relative. Spectra for the fossil faunas are constructed by adding together the weightings, by habitat type, calculated for each fossil species. The analysis of modern communities has shown that most modern habitats are identified by characteristic THI patterns. Examples are given in the next chapter. The advantages of this method are that the whole fauna is used; each species is assigned a range of possible habitats; the weighting of this range varies according to the closeness of its relationship to living relatives; and that relative abundance can be used.

The method is illustrated by table 3.2 and figure 3.2 which show the species weightings and the THI spectrum for the same hypothetical mammal community as that used in table 3.1 and figure 3.1.

Table 3.2. Taxonomic Habitat Index weightings for a hypothetical boreal forest community.

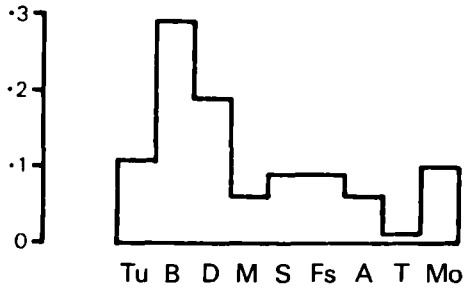
| Taxon | Habitat | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Tu | B | D | M | S | Fs | A | T | Mo |
| Erinaceus europaeus | – | – | ·5 | ·1 | ·1 | ·2 | – | – | ·1 |
| Sorex minutus | ·3 | ·3 | ·3 | ·05 | – | – | – | – | ·05 |
| Sorex araneus | ·2 | ·2 | ·2 | ·2 | – | ·1 | – | – | ·1 |
| Sorex sp. | ·09 | ·26 | ·14 | ·06 | ·08 | ·07 | ·05 | – | ·25 |
| Soricidae | ·05 | ·14 | ·18 | ·09 | ·07 | ·06 | ·11 | ·02 | ·28 |
| Neomys fodiens | ·2 | ·2 | ·2 | – | – | ·2 | – | – | ·2 |
| Talpa europaea | – | ·2 | ·5 | ·1 | ·1 | ·1 | – | – | – |
| Lepus timidus | ·35 | ·35 | ·05 | – | – | ·05 | – | – | ·2 |
| Lepus sp. | ·05 | ·24 | ·14 | ·02 | ·16 | ·02 | ·13 | ·14 | ·1 |
| Sciurus vulgaris | – | ·4 | ·4 | ·1 | – | ·1 | – | – | – |
| Pteromys volans | – | ·7 | ·1 | – | ·2 | – | – | – | – |
| Myopus schisticolor | ·15 | ·8 | – | – | – | – | – | – | ·05 |
| Clethrionomys rutilus | ·4 | ·45 | – | – | ·05 | ·1 | – | – | – |
| Clethrionomys sp. | ·08 | ·33 | ·28 | – | ·01 | ·04 | – | – | ·26 |
| Arvicola terrestris | ·2 | ·3 | ·2 | ·05 | ·1 | ·1 | – | – | ·05 |
| Ondatra zibethicus | – | ·6 | ·2 | – | ·1 | ·1 | – | – | – |
| Microtus agrestis | ·05 | ·4 | ·4 | ·05 | – | – | – | – | ·1 |
| Microtus oeconomus | ·4 | ·5 | – | – | – | ·1 | – | – | – |
| Microtus sp. | ·05 | ·1 | ·15 | ·07 | ·13 | ·08 | ·14 | ·01 | ·27 |
| Micromys minutus | – | ·15 | ·3 | ·05 | ·2 | ·3 | – | – | – |
| Apodemus sylvaticus | – | – | ·2 | ·2 | ·2 | ·2 | ·2 | – | – |
| Apodemus sp. | – | ·07 | ·21 | ·13 | ·12 | ·05 | ·02 | ·12 | ·28 |
| Muridae | – | ·05 | ·14 | ·1 | ·12 | ·04 | ·26 | ·09 | ·2 |
| Sicista betulina | – | ·4 | – | – | ·2 | ·4 | – | – | – |
| Canis lupus | ·15 | ·15 | ·15 | ·15 | ·15 | ·15 | ·05 | – | ·05 |
| Vulpes sp. | ·02 | ·02 | ·03 | ·03 | ·2 | ·06 | ·56 | ·01 | ·07 |
| Nyctereutes procyonoides | – | ·3 | ·3 | – | ·3 | – | ·1 | – | – |
| Gulo gulo | ·4 | ·4 | – | – | ·1 | – | – | – | ·1 |
| Mustela erminea | ·2 | ·2 | ·2 | – | ·1 | ·1 | ·1 | – | ·1 |
| Mustela nivalis | ·15 | ·15 | ·15 | ·15 | ·15 | ·15 | ·05 | – | ·05 |
| Mustela sp. | ·05 | ·24 | ·19 | ·02 | ·18 | ·06 | ·05 | – | ·21 |
| Martes martes | – | ·4 | ·4 | ·1 | – | – | – | – | ·1 |
| Meles meles | – | ·15 | ·2 | ·15 | ·15 | ·15 | ·1 | ·05 | ·05 |
| Alces alces | ·1 | ·7 | – | – | – | – | – | – | ·2 |
| Totals i | 3·64 | 9·85 | 6·41 | 1·97 | 3·27 | 3·08 | 1·92 | 0·44 | 3·42 |
| ii | ·11 | ·29 | ·19 | ·06 | ·09 | ·09 | ·06 | ·01 | ·1 |

Figure 3.2.

The Taxonomic Habitat Index pattern for the hypothetical boreal forest community listed in table 3.2 is shown. The scale refers to the average weighting for each habitat shown at ii in table 3.2. Comparison of this pattern with those given in figure 3.1 shows that the Taxonomic Habitat Index gives a much clearer indication than Habitat Spectra that the community comes from a boreal forest habitat.

The habitat abbreviations used are the same as those listed on p. 68 and in Appendix 5.

Figure 3.2. Taxonomic Habitat Index pattern of a boreal forest community.



iii. Discussion of methods weighting variability.

One of the conclusions of niche theory is that a species can survive in any habitat into whose niche space the species' niche can be incorporated. Methods such as Habitat Spectra and Taxonomic Habitat Index, which recognise that many species occupy a range of habitats are thus logical extensions of this aspect of niche theory. The Taxonomic Habitat Index weights both the variability of habitat preferences among extant species, and the degree of relatedness between extant species and their fossil relatives, while Habitat Spectra on the other hand, weight the degree of relatedness and take into account (but do not weight) the variability of habitat preferences.

One problem in the use of Habitat Spectra is that of how to assess the range of habitat types for the species in the fossil record. Unless there are clear morphological indications, or unless the species is extant, the only alternatives are to either take the range of a close living relative, or the range of all extant relatives contained within the lowest taxonomic level at which the fossil is related to living species. Of these two alternatives the first can be criticized on the grounds that there is no good reason to choose one living relative rather than another, although the choice may have considerable effect on the habitat range obtained, since even closely related species can differ

quite considerably in their distribution or preferences. The second alternative amounts to the same procedure as used in Taxonomic Habitat Index analyses. A further problem arises when all the habitats in a species range are taken into account. Since all are equally weighted, the relative importance of less-preferred habitats is apparently stressed too strongly. Habitat Spectra give much clearer results if the presence of these less-preferred habitats is ignored and in practice it has been found that habitats whose weighting for THI are 0.1 or less should be ignored for the purposes of constructing Habitat Spectra.

It also seems likely that the range of weighting used (1 through 6) for the degree of relatedness may be misleading. Species tend to be far more restricted in their distributions than genera to such an extent that a relative weighting of 2:1 rather than 6:5 would be preferable and it is possible that a logarithmic scale of weighting would give much better results.

By contrast, the Taxonomic Habitat Index method overcomes the problem of relative importance by numerically weighting each habitat in a species' range, and the effects of phylogenetic distance are allowed for by averaging the weightings of all species within a taxon. The use of averages also allows due regard to be paid to the level of variability found within each

taxonomic group. A fossil species whose range of habitats is extrapolated from a highly variable group will show no strong preference for any habitat type, whereas if all the species in a group share a preference for one habitat type, this fact will be reflected in the averaged weightings calculated for the fossil form.

Both these methods represent a positive advance over traditional indicators. Great importance is still placed on taxonomy, phylogeny, and a knowledge of the habits of living species, but both Habitat Spectra and the Taxonomic Habitat Index are logical extensions of niche theory, and both satisfy the conditions for the use of indicators. THI seems to be the better of the two methods because of the way variability in habitat preferences and phylogenetic relationships are weighted, and on balance it should be used in preference to HS or traditional methods whenever possible.

iv Data required for methods weighting variability.

The methods weighting variability, in common with all indicator methods, rely to an enormous extent on knowledge about the habits of living species. The Taxonomic Habitat Index is used in preference to Habitat Spectra throughout the rest of this work and for this reason the problems of gathering basic data for living species will be discussed with particular reference to THI. Data can be obtained from a number of sources such as published descriptions of a species' habits and preferences, personal and unpublished observations, and from distribution maps.

The weighting of habitats within a species' range is intended to reflect the frequency with which the species is to be found in each habitat (Nesbit Evans et al., 1981). This information often cannot be accurately determined, particularly from personal knowledge and published descriptions. Although these two sources usually give useful information about the actual habitat preferences of a species, unless the whole of the area over which it is distributed has been sampled, some of the less preferred habitats in which it is found may never be recorded. Distribution maps give complete coverage and they can be used as an objective way of weighting the habitat range by assessing the proportion of the species' total distribution that overlaps each habitat type on a standard vegetation map.

The distributions of many species coincide with areas of the major vegetation types and where a large part of a species' distribution overlaps a given vegetation type it might reasonably be assumed that the species lives in that habitat. The main drawback is that most vegetation maps show only the regional climatic climax habitats (see p.164) which conveys nothing about the biotope preferences or precise habitat preferences of the mammal species. Despite the fact that this technique is not wholly satisfactory it does have the advantage that it allows the habitat ranges of all species to be assessed in the same way.

Phylogenetic relationships also have to be taken into account. For practical purposes, the contribution of a fossil form is most easily weighted on taxonomic grounds. This obviously depends on current opinions about the relationship of the fossil to modern species, but it is comparatively rare that a fossil form cannot be assigned at least at genus or family level. It may often be impossible to identify the single most closely related modern species but it usually fairly simple, on taxonomic grounds alone, to identify the taxonomic group within which the fossil species has its closest relationships to living species.

The weighted distributions for 418 Palaearctic mammal species are given in appendix 3. Nine groups of Palaearctic habitats were recognised: Tundra; boreal forest; deciduous forest; mediterranean habitats; steppe; forest-steppe; dry-steppe, semi-desert and desert; tropical habitats; montane habitats. The weighted ranges were drawn up using distribution maps from Corbet (1978) supplemented by information from published sources where this was available. The weighted distributions for African tropical mammal species are shown in appendix 4. These are based on unpublished data kindly supplied by Dr. P.J. Andrews and Dr. E.M. Nesbit Evans. Five groups of habitats were recognised: Forest; woodland; bushland; grassland; semi-desert and desert. The weighted distributions for the mammals of these two regions were used to construct THI distributions both for modern communities (see chapters 4 and 5) and fossil faunas (see chapters 6 and 7).

c. Methods Using Microhabitat Preferences.

i. Biotope Spectra.

Biotope Spectra make use of species' microhabitat or biotope preferences and represent a second logical extension of niche theory into the realm of indicator methods. The greatest affinity of Biotope Spectra lies with the traditional indicator methods, that is, an association with a single invariable set of conditions rather than a weighted or unweighted range. However, although an association with a single habitat is a very poor reflection of the habits of living species, for Biotope Spectra the associations of species are described not in terms of habitats but in terms of the environmental conditions with which the species is usually associated. These can provide a reasonable approximation of the conditions associated with its fundamental niche. Many extant species can be found in a variety of different habitat types but usually in association with specific environmental conditions within those habitats. Their distribution is thus not determined by habitat types per se but by the occurrence of certain limiting factors within those habitats. These are species-specific conditions distinct from those necessary for the survival of all animals, and in many cases although no controlling variables can be isolated, a species will show strong affinities for certain conditions which can normally be used to define its biotope.

The Biotope Spectrum method works by defining for each species in a fossil fauna, the species-specific conditions necessary for its survival and/or the biotope with which it is usually associated. The biotopic requirements and associations of each species in the fauna can then be combined to build up a picture of the habitat in terms of its constituent biotopes. The advantages of this method are that it uses a more realistic model of the way species are distributed according to their adaptations; the whole fauna can be used and the biotopic associations of virtually any plant or animal species can be combined in one analysis; the habitat is described in terms of environmental conditions and not simply as an example of a recognised habitat type; different species can reflect quite diverse aspects of the environment which allows a varied and sometimes vivid picture to be built up.

All indicator methods suffer from the problem that the habits of fossil species are unknown and have to inferred from living forms. In the case of Biotope Spectra it is not always easy to determine the biotope requirements even for living species, and once this information is available there are a number of alternative ways in which it can be used. For instance, the biotope of a fossil species can be inferred either from the single closest living relative or from a group of close living relatives by taking into account either

the biotope with which the majority are associated, the range of biotope associations, or only the associations that all members of the group share in common. Taxonomic identity and a clear understanding of evolutionary relationships are thus of great importance and the method obviously works best where the fossil forms belong to extant species. Groups which do not evolve rapidly, and those in which biotopic requirements tend to be very restricted, are the most useful for constructing Biotope Spectra, and bird faunas, for instance, tend to give much better results than mammal faunas for both these reasons (see the Lazaret case study, chapter 6). However, the effectiveness of the method decreases rapidly with increasing geological age. A further drawback to the method is the fact that although a vivid impression of the habitat may be built up, this reconstruction is not an objective or formal description of the environment that can easily be compared with the reconstructions for other sites.

## 3. Population methods.

### a. Socioecology.

Jarman (1974) analysed the ecology, social organization and morphology of African antelope in terms of the relationships between body size, group size and the dispersion and availability of food items in the environment. He showed that both body and group size can be related to habitat choice and to aspects of behaviour such as reproductive strategy and the degree of sexual dimorphism (Janis, 1982). Jarman outlined five socioecological categories each associated with a different habitat type, which Janis (1982) was able to relate to a number of fossil ungulates. Given fossil material that is sufficiently well-preserved, it is possible to infer diet, body weight, dimorphism and perhaps even group size, sex ratio and age structure. These factors may then allow the socioecological behaviour and habitat preferences of the species to be determined. At present, the use of this method is restricted to sites which yield large numbers of animals belonging to groups whose socioecology is well documented. These restrictions mean that Socioecology is unlikely to become widely applied as a palaeoecological method.

b. Mean Body Mass.

Bergmann's rule states that within a given species, individuals living in colder climates will tend to have a greater body mass than those living in warmer climates. This suggests that changes in mean body mass of a species through time, or from place to place, may indicate climatic differences. If body mass can be correlated with temperature then it should be possible to use this method to provide direct evidence of past temperature fluctuations (Avery, 1982). Avery applied this approach to a number of species from the Quaternary period of South Africa and Tchernov (1968) demonstrated that size variation of Spalax ehrenbergi correlated with fluctuations in rainfall. The reader is referred to Avery (1982) for a fuller example of the kind of analysis that is possible. This method is only suitable for use at sites producing large samples of individuals for species whose body dimensions have a known relation with some evironmental variable. For this reason Mean Body Mass is not a method that is suited to widespread use.

c. Discussion of Population Methods.

The usefulness of Socioecology and Mean Body Mass as palaeoecological methods is always likely to be limited by two factors. Firstly, they both rely on characters possessed by some but not all species and secondly, even when a suitable species is present at a

site, a good deal of detailed information about the species is required before either of these methods can be used. However, it is possible that there are other characteristics of populations that could be used in a similar way. A number of fundamental niche specializations at the group level can be identified in the organisation of social groups and the behaviour of populations. Dobzhansky (1950) put forward the suggestion that in the tropics mortality is directed so that competitively superior genotypes and phenotypes survive, whereas in temperate regions it is independent of genotype and phenotype and the most successful species are those that can reproduce and increase their population size most rapidly. In the temperate zone, selection would thus favour high fecundity but in the tropics reproductive efficiency and competitive ability would be more important. MacArthur and Wilson (1967) coined the terms "r-selection" and "K-selection" for these two types of selection. The terms are derived from the growth curve or logistic equation where "r" refers to the intrinsic rate of increase of a population and "K" to the carrying capacity of the environment (Andrewartha & Birch, 1954).

No organism is ever wholly r-selected or K-selected and Pianka (1970) chose to visualize a continuum where the "r" endpoint represents a perfect ecological vacuum (with no competition or density

effects whatsoever), while the "K" endpoint represents a situation where the environment is saturated with organisms and density effects reach a maximum. Thus K-selection, which is favoured in stable environments where competitive ability is most important, leads to increasing efficiency to produce competitively successful organisms, whereas r-selected species are more common in unstable environments where random and sometimes catastrophic mortality favours the survival of species whose high reproductive capacity enables them to rapidly fill the ecologic vacuum. Most terrestrial vertebrates seem to be relatively K-selected, although even within the mammals species range along the r-K continuum (Pianka, 1970). Pianka outlined a number of characteristics of animals associated with each type of selection. Species that are r-selected tend to be short-lived, have small body masses, mature quickly, produce large numbers of offspring and have populations that fluctuate in size through time. K-selected species tend to have larger body masses, produce only a few offspring which mature slowly, have longer life-spans and generation lengths, and maintain stable populations in equilibrium at or near carrying capacity. Traits such as body size, population productivity and age structure can be quantified in animals from some fossil assemblages and by assessing the importance of r-selected and K-selected species in an assemblage it may be possible to draw conclusions about conditions in the environment.

## 4. Community Diversity Methods.

Whereas indicator methods rely on the adaptational responses of individual species, diversity methods use the responses of a higher level ecological unit such as the community in a way that does not regard individual species as diagnostic of particular environmental conditions. However, of the many ways of analysing communities only a few can be applied to the fossil record. Although there have been attempts such as that of Olson (1966) to reconstruct food webs, the information necessary for discovering the complex relations between populations and their environments is generally not available from the fossil record in sufficient detail. The "real" structure of an ecosystem is something that remains out of reach, but this complete structure is reflected in many aspects of the ecosystem that can be observed (Margalef 1963). It is therefore necessary to use features of the ecosystem that have a high likelihood of being preserved in the fossil record. Of the approaches that can be applied the most commonly used are heterogeneity, equitability and ecological diversity.

a. Equitability.

The degree of eveness in the abundance of species, known as equitability, can serve as a useful guide to the palaeoecology of a fauna or part of a fauna. For instance, rodents are a particularly useful group in the African Miocene. If within a taxon such as the rodents, there is high equitability in a single fauna with no species comprising more than 50%, then this suggests a complex niche structure like that found in forests, whereas if a single species dominates (perhaps comprising as much as 80% of the rodent fauna) this is taken to indicate a simple niche structure like that found in more open habitats (Andrews, 1973; Andrews & Van Couvering, 1975).

b. Heterogeneity.

High heterogeneity (a large number of equitably distributed species) is often considered to be a result of settled or favourable conditions, whereas low heterogeneity is indicative of an immature, disturbed or unpredictable ecosystem, or unfavourable climatic conditons. (Avery, 1982; Gingerich et al., 1980; Goulden, 1969). However, care must be taken since this observation was originally made for communities from single habitats, and it is doubtful whether it is reliable when used to interpret faunas from a single time horizon sampled across a whole sedimentary basin (e.g. Gingerich et al. 1980) where the fauna may well be drawn from a range of habitat types.

c. Ecological Diversity.

i. History and outline of the method.

Ecological diversity is a method of analysing fossil faunas and palaeocommunities which, like other diversity methods, does not rely on the use of indicator species. It is a recent approach which developed out of the concept of species richness and was first used as a palaeoecological technique by Andrews et al. (1979). Ecological Diversity works by assessing the adaptational structure of a community and then relating this to the community's habitat. The method relies on the fact that different habitats tend to be occupied by communities with different adaptational structures. Habitats can be described and compared in terms of the communities occupying them and by analysing the adaptational structure of a fossil fauna it is possible to determine its original habitat. Ecological Diversity and its derivative, Residual Diversity, are the only diversity methods dealt with in any detail in the rest of this thesis since they are the only methods that do not require quantitative data.

The history of the development of Ecological Diversity provides an interesting example of how techniques developed for neoecology can become useful to palaeoecologists. For a long time, ecologists studying geographical trends were mainly concerned with variation in species richness and heterogeneity rather

than the idea that this implied parallel changes in community structure. It was not until a paper by Fleming in 1973 that any attempt was made to formalize the comparison of community structure although it should be noted that Raunkaier used a similar method to analyse and compare the structure of plant communities in a series of papers in the early 1900's (see p. 156 and Raunkaier, 1934).

Fleming (1973) observed that several authors had documented a 2 to 2.5 times increase in the number of bird species resident in the tropics compared with similar habitats in temperate regions. This increase was attributed to various causes such as more precise habitat selection, greater vertical stratification in the foliage, and a greater relative stability of food resources, the latter implying differences in trophic structure beween temperate and tropical communities. Similar trends in the species richness of mammal communities in North America had been documented by Simpson (1964) and the purpose of Fleming's paper was to demonstrate differences in the trophic structure of living mammal communities from different latitudes. Fleming adopted an elegant approach based on a method of categorizing trophic levels and feeding zonations of mammals developed by Harrison (1962) in a study of tropical forest communities. Fleming added to Harrison's classes and classified all mammalian species

in his sample of seven communities according to their mammalian order, body weight, diet, and locomotor habits. Then for each habitat the proportion of the total fauna falling into each class of the taxonomic, weight, diet, and locomotor categories was calculated and plotted in the form of a histogram. Tests for significant trends were made using contingency tables and the equitability of each adaptational category (weight, diet, and locomotion) for each community was calculated and the results plotted in a three dimensional space in order to show structural similarities between the faunas. Fleming minimized the effect of habitat differences by selecting only "forest" communities from different latitudes but subsequent work by Nel (1975) and Andrews et al. (1979) documented changes in ecological diversity for different habitats from similar latitudes.

The next conceptual advance was made by Andrews et al. (1979) who realised that animals from the fossil record could be classified by order, body weight, diet and locomotor specializations in more or less the same way that Fleming had used for modern mammals.
The structure of a fossil fauna can then be analysed and compared with the structures of modern communities from known habitat types, and by this means it is possible to infer the habitat that was occupied by the fossil fauna.

Andrews et al. (1979) obtained a modern comparative sample by analysing communities from 23 modern African localities covering the whole gradient of tropical African habitat types. Some changes were made so that the method could be used for fossil faunas as well as modern communities. For instance, bats were omitted (as they are in this study) because they are so rarely found in fossil assemblages and the emphasis of classification of dietary and locomotor types was based on morphology rather than behavioural criteria which are unknown for fossils. Five African fossil faunas ranging in age from early Miocene to Pleistocene were analysed and their ecological diversity patterns compared with those from the 23 modern communities. Three of the faunas, Songhor, Fort Ternan, and Olduvai showed strong resemblance to modern lowland forest, woodland-bushland, and woodland-grassland habitats respectively. The remaining two, those from Rusinga and Karungu showed no obvious similarities to any of the modern tropical habitat types.

ii. Ecological Diversity model.

The accuracy and reliability of a scientific model is limited by the assumptions it makes. Ecological Diversity determines the adaptational structure of a community and relates this to the habitat. However, the model underlying this method has never been explicitly outlined and it is important that

the key assumptions on which it relies should be made clear.

Complete competitive exclusion with no overlap of niches is assumed, so that no area of niche space is occupied by more than one species. Since it is impossible to have two species occupying the same sector of niche space, species must therefore have additive effects. The competitive exclusion principle is generally accepted among ecologists, at least as a working rule. However niche overlap seems to be quite common so that complete exclusion is not the rule in nature.

The assumption is made that all the niche space available in the habitat is filled. This, combined with the first assumption, means that the community completely maps the niche space available in the habitat and that the adaptational structure of the community can be regarded as an expression of this available niche space. If this were not the case then any unused space would be intangible and variation between the ecological diversity patterns of different habitats could be ascribed to variability in the amount of niche space that is actually used. Whether or not all the niche space available is actually utilized is largely to do with the unique history of the area in question, a factor that cannot easily be taken into account.

All species are taken to be equally important. The importance of the species to the ecological diversity of the community is independent of the species importance in the community in terms of measures such as biomass, relative abundance and productivity.

It is also accepted that the effect of the habitat is limited to the amount of niche space available. Effects of size of habitat "islands" and the extent to which they are isolated from donor habitats cannot be taken into account.

These assumptions discount possible sources of variation so that the source of significant variation between communities can be defined as differences in the amount of niche space available within the habitat and in the way it is partitioned among the species present. The habitat can then be described in general terms by the community adapted to live in it. As a very simple example, for instance, arboreal species are confined to habitats with trees, and browsing herbivores are much more common in woodland than in open habitats, while the reverse is true of grazers.

It is also possible to outline the basic conditions that have to be satisfied before Ecological Diversity can be used as a palaeoecological method. Ecological diversity distributions describe the niche

space available within a habitat which means that there are three relationships involved. Firstly, there is the relationship between the habitat and the niche space available, secondly that between the available niche space and the ecological diversity distribution and thirdly the relationship between a palaeocommunity and the fossil assemblage derived from it. In practice this means that a modern comparative sample is required which consists of a series of habitat types which can be clearly defined in terms of the ecological diversity of the mammal communities occupying them. One important requirement is that the mammal communities associated with the habitats in the modern sample should accurately map the niche space available. If the community is incomplete or impoverished, then its adaptive structure will give a misleading impression of the niche space that is actually available in the habitat. Unfortunately, some modern communities do appear to be impoverished when compared with their fossil counterparts and this causes problems particularly with temperate communities, especially those from areas where there are high densities of human population.

As far as a fossil assemblage is concerned it must be representative of the community from which it originated. This allows the adaptive structure of the palaeocommunity to be determined and compared dire tly with communities from known habitats in the modern

sample. Unfortunately, fossil faunas are often found to have lost a considerable number of species during the process of fossilization. When this is the case, the ecological diversity of the fossil assemblage cannot be compared directly with that of modern commmunities.

It is appropriate at this point to mention taphonomy and its importance for palaeoecology. Taphonomy means "the laws of burial" and it is a field of study that serves to focus all the varied interests that describe and analyse how organisms become fossils (Behrensmeyer & Hill, 1980: preface). An enormous drawback of most palaeoecological methods is that they have to use fossil assemblages which are only samples drawn from palaeocommunities. These samples can result from any number of processes which bias the original record. Taphonomy is not independent of information on biological processes, but since it does not focus directly on the relationship between living organisms and their environments it cannot, strictly speaking, be considered a palaeoecological method. However, by throwing light on the conditions and processes of bone accumulation, taphonomy makes natural sampling processes more understandable and provides a means of reconstructing original communities from fossil assemblages. Palaeoecological methods can then be used to interpret these reconstructed communities, thus in many instances, some kind of taphonomic analysis is an essential prerequisite to any palaeoecological study.

The need for preliminary taphonomic conclusions can be overcome by using palaeoecological methods that do not rely on the whole community being preserved. Taphonomic biases have predictable effects on a number of palaeoecological methods and these methods can be applied directly to incompletely preserved communities without the need for any taphonomic information. It is possible, for instance, to allow for some of the effects of partial preservation of the palaeocommunity by assessing the residual diversity of an assemblage as described later in this chapter. The effects of species loss on various palaeoecological methods is illustrated by a series of simulations in chapter 5.

iii Mathematical measures.

All the ecological diversity analyses published to date have used the Shannon-Weiner function to estimate diversity. This function is derived from information theory and it is usually used in ecological applications to measure heterogeneity (see above, p.48 and Pielou, 1966; 1977). The function is sensitive to two variables, firstly the number of discrete classes used, and secondly the equitability of the sample measured in terms of the proportion of the total community falling in each class. Since the same number of weight, diet, and locomotor classes is used in the analysis of each community, estimates of diversity using the Shannon-Weiner function are sensitive only to

proportional differences between the faunas and not to any differences in their absolute size. The number of species in a community is an important characteristic and one of the implications of the Ecological Diversity model is that a community with more species should be regarded as more diverse. Since communities can show striking differences in size, methods which take the absolute number of species into account are likely to be more effective in differentiating between communities from different habitat types. For both of these reasons it is more appropriate to use Brillouin's formula which measures diversity in terms of absolute numbers (see p.49 ).

However, a much more important point that has apparently been overlooked is that it is not sufficient merely to compare the mathematical diversities of two communities. Two communities that are equally diverse in terms of their equitability or heterogeneity may have distributions that differ quite considerably across their respective classes. It is better to measure the difference in diversity using an expression such as:

$$H'diff. = -\sum_{i}^{s} \frac{p_i + q_i}{2} \ln \frac{p_i + q_i}{2} + \frac{1}{2}\left[\sum_{i} p_i \ln p_i + \sum_{i} q_i \ln q_i\right] \quad (3.1)$$

(where s is the number of ecological diversity classes; $p_i$ = the proportion of the first community falling in the ith class; $q_i$ = the proportion of the second community falling in the ith class; $\sum p_i = 1$; $\sum q_i = 1$).

This is an expression based on the Shannon-Weiner function which compares communities class by class and does not allow the case of two quite dissimilar distributions of equal diversity to pass undetected (MacArthur et al., 1966). A function such as this simply measures the distance between two communities in a "diversity hypervolume". In fact any distance measure becomes a measure of diversity difference provided that it is based on some characteristic of the communities that is a reasonable expression of their diversity. Perhaps the easiest distance function to use is euclidean distance which is given by:

$$D = \sqrt{\sum_{i}^{s}(p_i - q_i)^2} \qquad (3.2)$$

or:

$$D = \sqrt{\sum_{i}^{s}(N_i - M_i)^2} \qquad (3.3)$$

(where s, $p_i$ and $q_i$ are as in equation 3.1; $N_i$ = the number of species in the ith class of the first community and M = the number of species in the ith class of the second community.)

The use of euclidean distance has two real advantages. Firstly, the same mathematical expression can be used for distances based on either proportions (equation 3.2) or absolute numbers (equation 3.3) and secondly, euclidean distances are free from the side effects of logarithms and factorials which are suffered

by information functions. Euclidean distance is used to compare ecological diversity patterns throughout the rest of this work. When absolute numbers are used the function becomes sensitive to differences in the size of communities and differences in the shape of Ecological Diversity distributions. The use of proportions eliminates the effects of size and only compares distributions in terms of their shapes. In either event, the use of distance statistics also has the advantage that it allows ordination and grouping techniques to be performed on similarity matrices obtained from sets of samples. Use has been made of this technique to show that modern habitats can be distinguished on the basis of the ecological diversity of their associated communities (see chapter 4, pp. 225 and 273).

Table 3.3. Ecological Diversity classes.

Weight classes

| | |
|---|---|
| A | 0 - 0·1 kg. |
| B | 0·1 - 1 kg. |
| C | 1 - 10 kg. |
| D | 10 - 50 kg. |
| E | 50 - 100 kg. |
| F | 100 - 200 kg. |
| G | 200 - 400 kg. |
| H | over 400 kg. |

Diet classes

| | |
|---|---|
| I | insectivorous |
| FR | frugivorous |
| HB | browsing herbivore |
| HG | grazing herbivore |
| CA | carnivorous |
| O | omnivorous |
| HF | herbivore-frugivore |
| HI | herbivore-insectivore |

Locomotor classes

| | |
|---|---|
| LG | large ground adapted (confined to ground) |
| SG | small ground adapted (facultative climber) |
| AR | arboreal |
| S | scansorial (confined to trunk and large branches) |
| AQ | aquatic |
| FO | fossorial (burrowing) |
| AE | aerial |

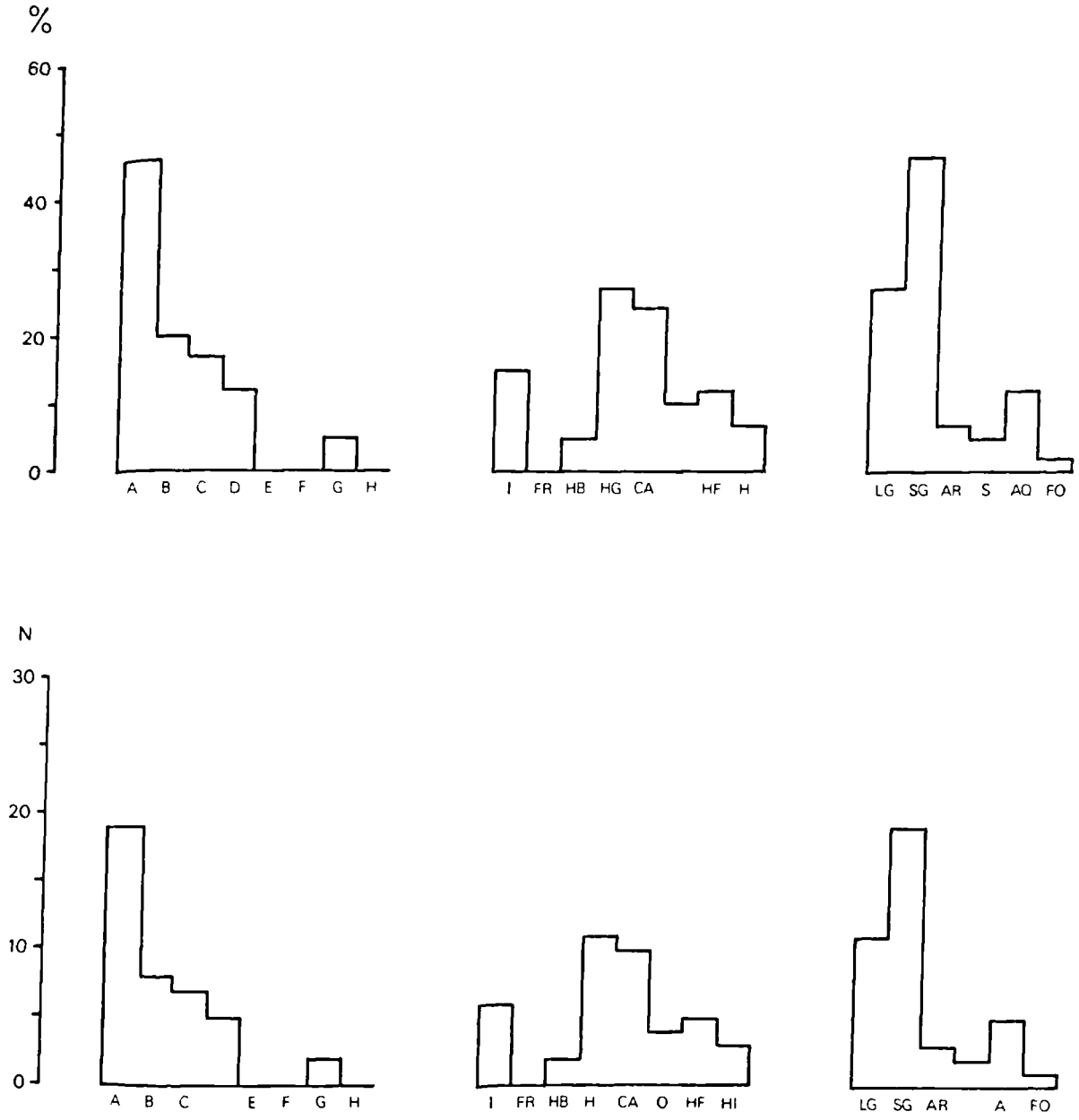
Table 3.4. Ecological Diversity classes of species in a boreal forest community.

| Taxon | Classifications | | |
|---|---|---|---|
| | Weight | Diet | Locomotor |
| Erinaceus europaeus | B | HI | SG |
| Sorex minutus | A | I | SG |
| Sorex araneus | A | I | SG |
| Sorex minutissimus | A | I | SG |
| Sorex caecutiens | A | I | SG |
| Neomys fodiens | A | I | AQ |
| Talpa europaea | A | I | FO |
| Lepus capensis | C | HG | LG |
| Lepus timidus | C | HG | LG |
| Sciurus vulgaris | B | HF | S |
| Pteromys volans | B | HF | AR |
| Myopus schisticolor | A | HG | SG |
| Clethrionomys glareolus | A | HG | SG |
| Clethrionomys rufocanus | A | HG | SG |
| Clethrionomys rutilus | A | HG | SG |
| Arvicola terrestris | B | HG | SG |
| Ondatra zibethicus | C | HG | AQ |
| Microtus agrestis | A | HG | SG |
| Microtus oeconomus | A | HG | SG |
| Microtus arvalis | A | HG | SG |
| Micromys minutus | A | HI | AR |
| Apodemus sylvaticus | A | HF | SG |
| Apodemus agrarius | A | HF | SG |
| Rattus norvegicus | B | HF | SG |
| Mus musculus | A | O | SG |
| Sicista betulina | A | HI | AR |
| Castor fiber | D | HB | AQ |
| Canis lupus | D | CA | LG |
| Vulpes vulpes | C | CA | LG |
| Nyctereutes procyonoides | C | O | LG |
| Ursus arctos | G | O | LG |
| Gulo gulo | D | CA | LG |
| Mustela erminea | B | CA | SG |
| Mustela putorius | B | CA | LG |
| Mustela nivalis | A | CA | SG |
| Mustela lutreola | B | CA | AQ |
| Martes martes | C | CA | S |
| Meles meles | D | O | LG |
| Lutra lutra | C | CA | AQ |
| Felis lynx | D | CA | LG |
| Alces alces | G | HB | LG |

Table 3.5. Ecological diversity of a boreal forest community.

| | N | % |
|---|---|---|
| Weight classes | | |
| A | 19 | 46·3 |
| B | 8 | 19·5 |
| C | 7 | 17·1 |
| D | 5 | 12·2 |
| E | 0 | 0·0 |
| F | 0 | 0·0 |
| G | 2 | 4·9 |
| H | 0 | 0·0 |
| Diet classes | | |
| I | 6 | 14·6 |
| FR | 0 | 0·0 |
| HB | 2 | 4·9 |
| HG | 11 | 26·8 |
| CA | 10 | 24·4 |
| O | 4 | 9·8 |
| HF | 5 | 12·2 |
| HI | 3 | 7·3 |
| Locomotor classes | | |
| LG | 11 | 26·8 |
| SG | 19 | 46·3 |
| AR | 3 | 7·3 |
| S | 2 | 4·9 |
| AQ | 5 | 12·2 |
| FO | 1 | 2·4 |

Figure 3.3 Ecological diversity pattern of a boreal forest community.



d. Residual Diversity.

i. Outline of the method.

Chance effects which result in the loss or addition of species during fossilization mean that the apparent adaptational structure of a palaeocommunity is artificially altered by non-ecological factors. There is no intrinsic reason why fossil faunas cannot be compared directly with modern communities, and some faunas are complete enough to be treated exactly like a modern community. However, in the majority of cases the intervention of taphonomic factors results in faunas that are not sufficiently representative of the original palaeocommunities, and in practice all faunas have to be treated as potentially unrepresentative. Under these circumstances a technique is required which can be used to interpret incomplete communities. A new method, which is designed to interpret the residue of taphonomic influences, was developed by the author during the course of this research. Following a suggestion made by Dr. Peter Andrews, this method is now known as Residual Diversity.

Two basic types of bias are possible in the fossil record, firstly, the loss of species from a sample derived from a single habitat (which is the most common type of taphonomic bias) and secondly, the mixture of species derived from different habitats, usually the result of a sedimentary environment with a

catchment area covering more than one habitat or, since fossil faunas are rarely contemporaneous, the result of time transgressive sampling during a period of environmental change. Since the loss of species appears to be the most common effect, the majority of the following discussion is with reference to species loss.

The probability of a species being preserved in the fossil record depends mainly on where members of a population die, (that is, where in relation to specific sedimentary conditions) how often they die, and on the durability of their remains. Biases tend not to affect all species equally and one of the most important influences is body size which can have several effects. Small species commonly have much greater population densities and higher death rates than large species, both of which will make them more likely to be represented than large species (Western 1980). However, the bones of small animals are more easily overlooked during excavation and collection and more easily reduced to unidentifiable fragments by excavators, predators, and natural processes. All these factors may result in the probability of successful recovery and identification of a species becoming greater with increasing body size. It should also be noted that as far as hominids are concerned, small mammals are not common food items and are not

usually recovered in large numbers from the occupation levels at archaeological sites. In contrast to this, predator assemblages are known from a number of sites which consist almost solely of small mammals (Avery, 1982; Mellett, 1974; see also Behrensmeyer and Dechant Boaz, 1980).

Preservational biases such as these make distance functions unreliable as measures of differences in ecological diversity. Functions using proportions and absolute numbers are affected in different ways. Those which use absolute numbers have the advantage that biases only affect those classes that have lost species whereas if proportions are used, the proportionate composition of all classes is affected. The use of distance measures based on proportions to measure diversity assumes that the proportionate composition of the fauna is not affected by taphonomic biases. This will only rarely be true since the proportionate composition of a fauna stays the same only when the loss of species is completely random. When absolute numbers are used, the loss of species reduces the size of a fauna and increases its overall similarity to smaller communities irrespective of the similarity of their adaptational patterns. The best way of getting round this last problem is to correct for that portion of the euclidean distance due solely to difference in size between the two communities. This is calculated by

"topping-up" all classes in the fossil fauna that contain less species than their equivalents in the modern community until the fossil fauna contains the same number of species overall as the modern community. This eliminates any size difference and the distance then calculated (using absolute numbers of species in each class) expresses the residual diversity of any classes in which the fossil fauna has more species than the modern community. This is not a reconstruction of the original adaptational pattern of the palaeocommunity but it represents an estimate of the minimum possible distance between the two communities. This residual diversity distance can be plotted against a distance between the two communities based on proportions before "topping up". When this is done for the distances calculated between a fossil fauna and a series of modern communities, a scatter of points is obtained whose configuration can be used to interpret the habitat type once occupied by the fossil fauna.

The method is designed to deal with fossil faunas that have suffered species loss during the process of fossilization. Classes in which the fossil fauna contains less species than the modern community with which it is being compared could arise in one of two ways. This could either be the result of species loss during fossilization reducing an originally large number of species in a given class to a low number after

fossilization, or alternatively it may be the result of an original ecological difference whereby the fossil fauna contained fewer species in a given class than the modern community even before fossilization. Thus a deficit is equivocal since it could be the result of either an original ecological difference or the loss of species during the formation of the fossil assemblage.

The consequences of an excess of species in a given class are in complete contrast to this. Since an excess cannot arise by species loss (which is the process being considered here) then it must reflect an original ecological difference. The fauna could, of course, originally have had an even greater excess than it displays after species loss, but it could not have had less species. It follows, therefore, that it must always have had more species in that class than the modern community with which it is being compared. The excess consequently indicates a character that is necessarily of ecological and not taphonomic origin.

ii Mathematical measures.

The basic form of the distance functions used to analyse the Residual Diversity of a fossil fauna was outlined above (see p.100). In the two dimensional Residual Diversity plots (such as that shown in figure 3.4ii and similar figures) the axes represent two slightly different distance measures both based on euclidean distance. The horizontal axis (labelled "Dp") represents a measurement of the difference between the two communities in terms of the proportion of each community falling in each class of the ecological diversity distribution (see p.100 and equation 3.2).

$$Dp = \sqrt{\sum_{i}^{s}(p_i - q_i)^2} \qquad (3.4)$$

(where s is the number of ecological diversity classes; p = the proportion of the first community occurring in the ith class and q = the proportion of the second community occurring in the ith class; $\sum_{i}^{s} p_i = 1$; $\sum_{i}^{s} q_i = 1$).

Since the distance function expressed in equation 3.4 is based on proportions and no account is taken of the total number of species in the communities, it is thus a measure of the difference in shape of the two ecological diversity distributions.

The distance represented on the vertical axis (labelled "De") is based on the absolute number of species in each class rather than the proportion of the whole community in each class (see p.100 and equation 3.3).

$$De = \sqrt{\sum_{i}^{s}(N_i - M_i)^2} \qquad (3.5)$$

(where s is the number of ecological diversity classes; $N_i$ = the number of species in the ith class of the first community and $M_i$ = the number of species in the ith class of the second community.)

This function is calculated after the fossil fauna has been topped-up to contain the same number of species as the larger modern community which eliminates the effect of differences in species richness. Only classes containing a deficit of species are topped -up and once the fossil fauna contains the same number of species as the modern community, it will normally have some classes in which there are more species than in the same classes in the modern community and some in which there are less. Since it is the classes with excess species which are regarded as significant, the effect of classes in which the fossil fauna contains less species has to be minimized. This is achieved during the process of topping-up by distributing the deficit as equitably as possible between the classes

involved. In cases where the fossil fauna contains more species than the modern community at the outset, no topping-up is performed.

The two distance functions Dp and De are calculated between a base fauna, which is usually a fossil fauna, and each of the communities in a modern comparative sample. The distances between the base fauna and each modern community are plotted against each other and the scatter of points obtained is an aid to the interpretation of the structure of the base fauna. The pattern also varies predictably with species loss as demonstrated in the simplified example that follows and also in chapter 5.

iii Simple example of Residual Diversity.

In the simplified example presented here, three hypothetical communities are used; two of these are modern communities (one from "forest", the other from "bushland") and the third a fossil community from an unknown habitat. All three coincidentally consist of 20 species each of which is classified into one of two mutually exclusive ecological diversity classes "P" and "Q".

The forest community has 15 species which fall in class P and 5 that fall in class Q (i.e. 75% of the community are P species and 25% Q species). The bushland community has 5 species in class P and 15 that fall in class Q (i.e. 25% are P species and 75% Q species). The two communities thus have quite distinct ecological diversity patterns which are easily distinguished from each other. The fossil fauna (which is of course from an unknown habitat) is identical in both the size and shape of its ecological diversity pattern to the community associated with the forest habitat. The ecological diversity profiles of the three communities are illustrated in figure 3.4i.

In the figures that follow, the effects of losing species from the fossil fauna are illustrated and described.

Figure 3.4 Residual Diversity of an unbiased fossil fauna.
Figure 3.4i

The ecological diversity patterns of the two modern communities and the complete fossil fauna are shown. The forest community has 15 species in class P and 5 in class Q, while the bushland community has 5 species in class P and 15 in class Q. The fossil fauna when complete has the same profile as the forest community.

Figure 3.4ii

The distances obtained from the comparison of the fossil fauna and the two modern communities are used to plot figure 3.4ii. The Dp distance between the fossil fauna and the forest community, Dp (fossil-forest), is zero since the two distributions are exactly the same shape. The distance De (fossil-forest) is also zero since there are no classes in which the fossil fauna has more species than the modern community. The resulting point (labelled "f") has coordinates 0,0 and falls at the origin.

The point corresponding to the bushland community does not fall at the origin. Since the fossil and bushland distributions are different in shape, the distance Dp (fossil-bushland) has a positive value [1]. Furthermore, since the fossil fauna has an excess of 10 species in class P compared with the bushland community, the distance De (fossil-bushland) also has a positive value. This means that the bushland point (labelled "b") falls somewhere in the two dimensional space described by the axes and not at the origin.

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[1] All values on both axes, excluding values of zero are arbitrarily assigned in this example.

Figure 3.4i.

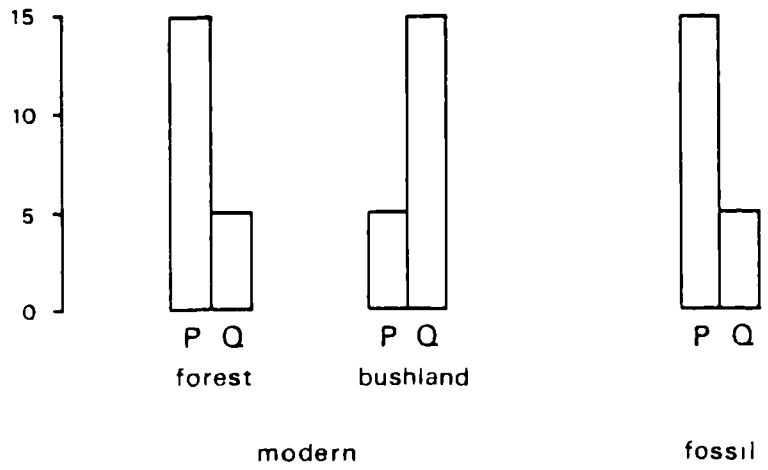



Figure 3.4ii.

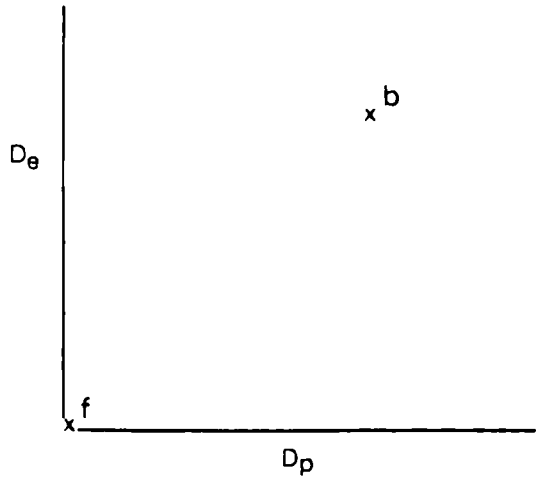


Figure 3.5 Effects of species loss from class P.

Figure 3.5i

This figure shows the consequence of the loss of species from class P of the fossil fauna. As shown in figure 3.5i, 5 species have been lost from class P leaving the fossil fauna with 10 species remaining in class P and 5 species in class Q.

Figure 3.5ii

After the loss of species from class P of the fossil fauna the fossil and forest distributions are no longer the same shape and the distance Dp (fossil-forest) becomes greater than zero. The value of De (fossil-forest) remains zero since the fossil fauna still has no classes which contain more species than the modern forest community. The net effect of these changes is to push the forest point "f" horizontally to the right.

The bushland point "b" also shows some movement, but the loss of species from class P of the fossil fauna affects the fossil-bushland distances differently from the fossil-forest distances. The value of Dp (fossil-bushland) falls because class P now forms a relatively smaller proportion and Q a relatively larger proportion of the whole fauna than was previously the case. This means that the shape of the fossil fauna is now more similar to the bushland pattern than it was formerly. Furthermore, the excess of species in class P has also been reduced from 10 to 5, which reduces the value De (fossil-bushland). The overall effect of these changes is to move the point "b" downwards and to the left as shown.

Figure 3.5i.

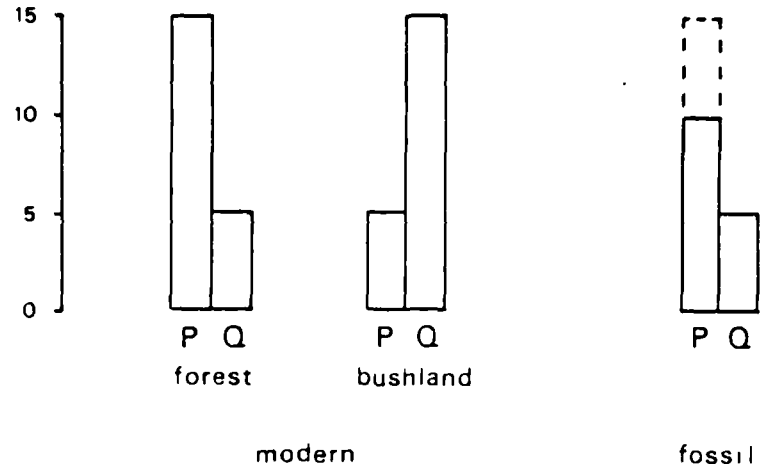



Figure 3.5ii.

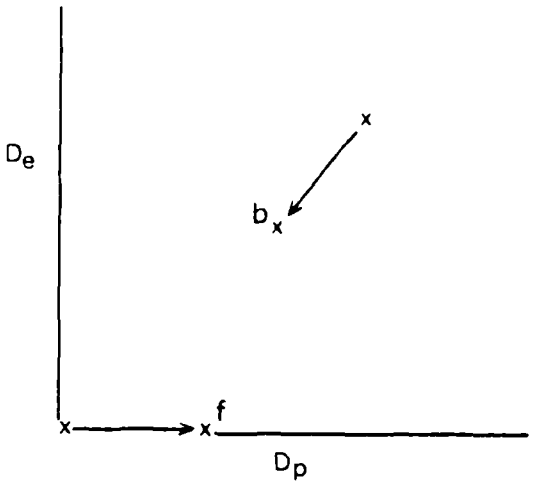
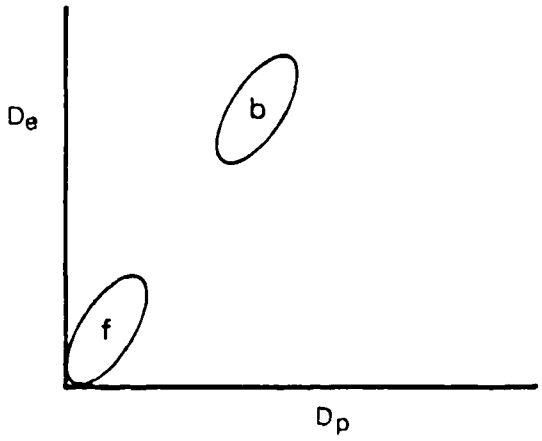


Figure 3.6 Summary of the effects of species loss from class P.

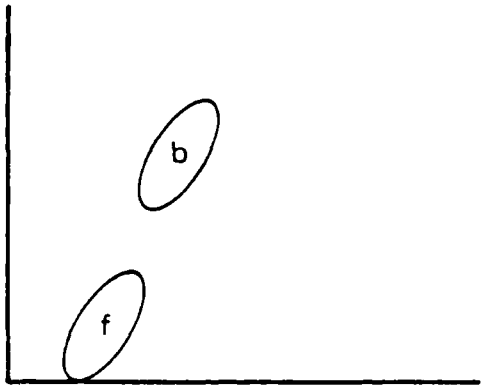
In practice the base fauna is normally compared with a modern comparative sample consisting of a number of modern communities from a variety of habitat types. The communities associated with each habitat type will tend to form groups of points, which under ideal circumstances will take the form of elliptical clusters as shown in figure 3.6. Under the conditions of species loss described in figure 3.5 (i.e. loss of species from class P) the elliptical clusters corresponding to a number of forest and bushland communities will behave in exactly the same way as the single points "f" and "b" in figure 3.5ii. Figure 3.6 shows four stages in a sequence resulting from the progressive loss of species from class P. The ellipses are shown to start from an original position on an axis passing through the origin (a state which is sometimes observed in the Residual Diversity patterns of modern communities). During the loss of species the forest group gradually moves horizontally to the right, while the bushland group moves downwards and to the left. This results in the final pattern (figure 3.6iv) where the bushland group lies nearer the origin than the forest group, in spite of the fact that the fossil fauna before species loss was identical in structure to a forest community.

Figure 3.6.

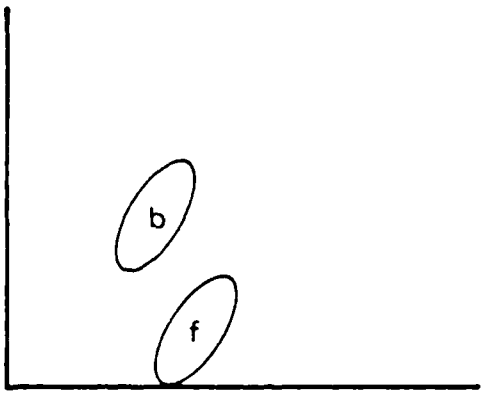
3.6i




3.6ii




3.6iii




3.6iv

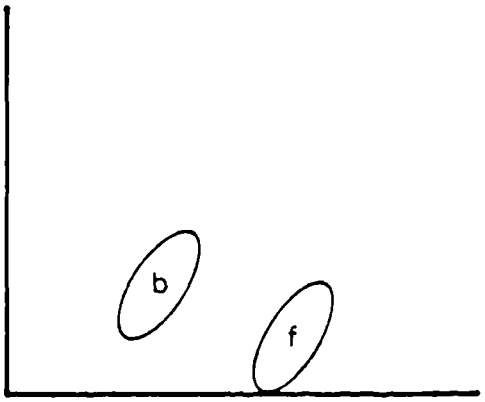


Figure 3.7 Effects of species loss from class Q.

Figure 3.7i

This figure shows the effects of the loss of species from class Q of the fossil fauna. These effects are quite different from those resulting from the loss of species from class P. As shown in figure 3.7i, 3 species have been lost from class Q leaving the fossil fauna with the original 15 species in class P and only 2 species remaining in class Q.

Figure 3.7ii

The loss of species from class Q means that the fossil and modern forest distributions are no longer the same shape which gives Dp (fossil-forest) a positive value. De (fossil-forest) has a value of zero since the fossil fauna still has no classes which contain an excess of species compared with the modern forest community. The net effect of the loss of species from class Q is thus to push the forest point "f" horizontally to the right.

As far as the bushland community is concerned, the fossil fauna only has an excess of species in class P, such that the loss of species from Q cannot affect the value of De (fossil-bushland) which therefore remains the same as before. However, the loss of these species also means that the two distributions are now less similar in shape than previously, which has the result that Dp (fossil-bushland) is increased in value. The overall effect is thus to move the bushland point "b" horizontally to the right as shown.

Figure 3.7'.

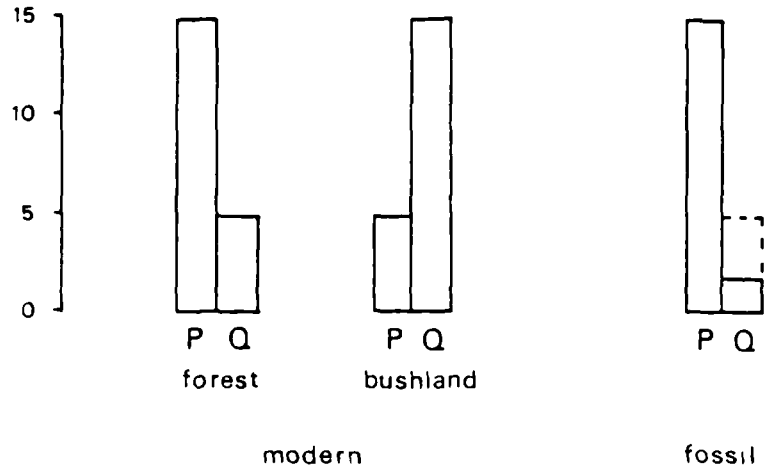



Figure 3.7ii.

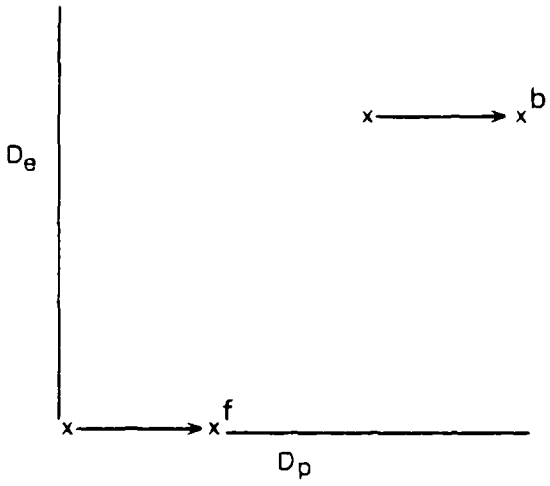
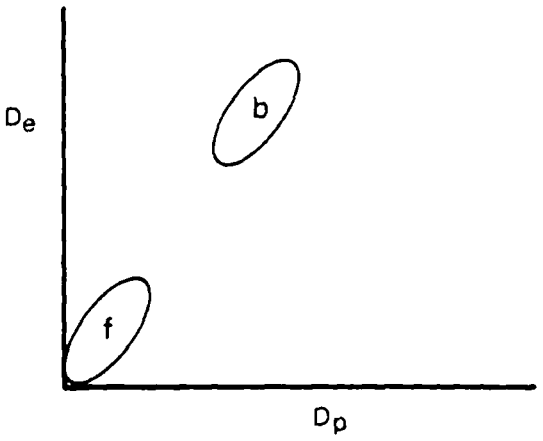


Figure 3.8 Summary of the effects of species loss from class Q.

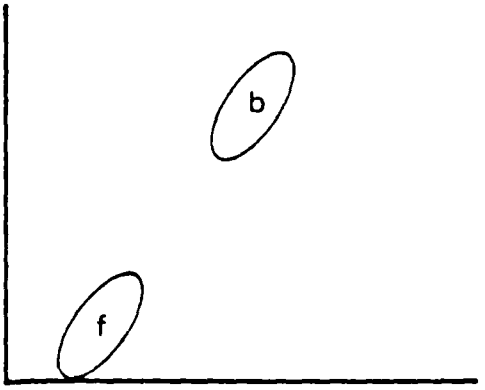
The two points "f" and "b" are once again replaced by ellipses representing clusters of points, the resultant series of stages can be seen in figure 3.8. The two clusters maintain their original relative positions as shown in figure 3.8i while moving horizontally to the right.

Figure 3.8.

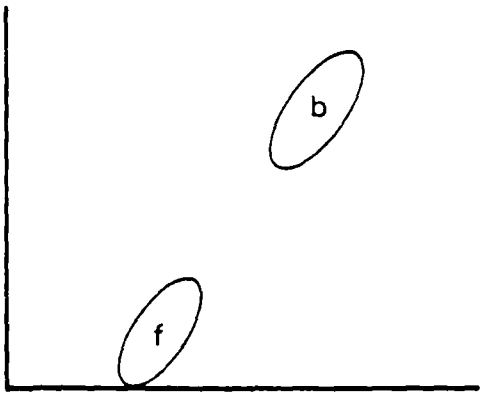
3.8i



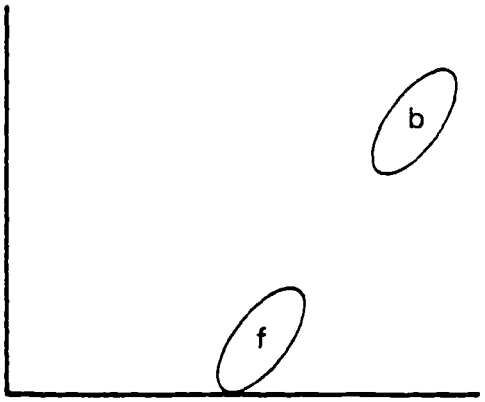

3.8ii




3.8iii




3.8iv



iv. Conclusions.

It can be seen from the simplified example described above that the loss of species from a community has a predictable effect on the residual diversity pattern, which depends on two interdependent factors. Firstly, the original structure of the base community, and secondly, the residual structure of the base fauna, which is determined by the species that remain after biasing. The relation between these is determined by what species are lost from the community.

It should be noted that in the example above, if the fossil fauna had resembled the bushland community, then groups "b" and "f" in the unbiased pattern would have been reversed. The effects of the loss of P and Q species would also have been reversed, but the same general trends would have been observed.

It can be seen from a brief comparison of figures 3.6 and 3.8 that the sequences corresponding to the loss of P species and Q species are quite different. However, in spite of this, the pattern after loss of species can still indicate the original habitat of the base fauna before any biases were introduced. With particular reference to figure 3.6iv, where the bushland group is nearest the origin, had it not been possible to show that this position is a natural consequence of the loss of species from class P of a fossil fauna derived from

a forest community, this pattern would probably have been interpreted as showing that the fossil fauna actually represented a bushland community. Although by this stage in the sequence the base fauna is more similar to modern bushland communities in most respects, it is important to realise that this is the result of taphonomic effects and is not due to any original similarity of ecological structure.

The example presented above is purposely simplified and in practice the situation is a great deal more complex. For instance, modern communities are not usually so distinctively different from each other as the two communities in the example. There is usually a range of community types, each of which behaves in a different way. Furthermore, in practice, there are 8 weight classes, 8 dietary classes and 6 locomotor classes, which unlike the classes P and Q in the example, are not mutually exclusive. It is possible, of course, to use weight or diet or locomotor classes alone, but in practice, community structure is best expressed by all three categories together and residual diversity patterns based on all three give much clearer results.

Species loss in practice is rarely as non-random as that illustrated above. Random loss would result in vertical collapse with no horizontal movement. In other words, the importance of classes with excess species

would be reduced, but the shape of each distribution would be unchanged. It also has to be noted that because of the relationship between weight, diet and locomotor classes, the degree of randomness in one class may not be matched by the same degree in other categories. Thus, what may be completely non-random loss with respect to weight classes might result in apparent randomness in the way species are lost from dietary or locomotor classes. In practice therefore, it is to be expected that any species loss is likely to be accompanied by some degree of horizontal movement in the residual diversity pattern.

In spite of all these complicating factors, the general principles outlined above are equally sound when applied to real fossil faunas and modern communities. In comparisons between the base fauna and modern communities any class in which the base fauna has a deficit of species is not necessarily ecologially significant, but classes with an excess of species do reflect an ecologically significant characteristic of the base fauna. Real fossil faunas and modern communities can thus be treated in the same way as shown in the simplified example by being compared in terms of differences in shape of their ecological diversity distributions and the significance of excess species. This is illustrated by simulations based on modern communities shown in chapter 5.

e. Classification for Ecological and Residual Diversity.

Ecological and Residual Diversity require a threefold classification of species according to body weight, dietary habits and locomotor specializations. Since both these methods have to be used with modern and fossil species, every effort was made to treat both sets of animals in the same way in order to make the information available for each group as comparable as possible. Living animals can be classified by live body weights and observation of their dietary and locmotor behaviour, but for most fossil species evidence about their adaptations can only be inferred from the morphology of teeth and skeletal parts and estimates of body size. Every attempt has been made to classify modern species using morphological criteria of the kind that would be preserved in fossils. However, observed behaviour also has to be taken into account since the meaning of some morphological characteristics remains obscure if they are not viewed in the light of the behaviour patterns the species are known to perform. It is impossible, in the space available here, to give an exhaustive key to the diagnosis of Ecological Diversity classes for all species, but the following notes give an idea of the procedures that were followed in the classification of living and fossil species. It should be noted that the earliest studies using Ecological Diversity also made use of taxonomic

diversity at the ordinal level. Taxonomic diversity was not used in this study since one of the fundamental principles behind diversity methods such as Ecological and Residual Diversity is that taxonomic identity is not an ecologically significant characteristic.

i. Weight.

Weight classes:

| | |
|---|---|
| A 0 - 0.1kg. | B 0.1 - 1kg. |
| C 1 - 10kg. | D 10 - 50kg. |
| E 50 - 100kg. | F 100 - 200kg. |
| G 200 - 400kg. | H over 400kg. |

Sources:

Modern species - From published records of live body weights and weight ranges, estimated from skull, tooth or post-cranial measurements, or estimated by examination of the skull or other body parts.

Fossil species - Fstimated from skull, tooth or post-cranial measurements, or by examination of skull and other body parts.

Apart from records of live body weights, none of the other methods used provides an absolutely precise estimate of body size in every case. No directly measured body weights are available for fossil species. It is therefore necessary to fall back on estimates based on preserved body parts whose relationship to body weight has been "calibrated" with modern species. Several studies have been published on the relationship between body size and body dimensions, for instance, Kay (1975), Gingerich (1977) and Creighton (1980). In some cases post-crania provi le better estimators of

body weight, for instance, in ungulates (K.M. Scott, cited by Janis, 1982) and probably also in Primates (L. Aiello, pers. comm.). However, since the weight classes used for Ecological Diversity have large ranges (with the exception perhaps of classes A and B), nearly all specimens fall into unambiguous weight classes even if the estimated body weight cannot be precisely determined. Where a species was found to span more than one class it was generally assigned to the class in which most of its weight range fell (provided the end points of the range were not obviously anomalous). Where this guideline could not easily be applied, the lower weight class was used on the grounds that the majority of the population was likely to fall at the lower end of the distribution (immature individuals, and one of the sexes in dimorphic populations), whereas the upper end will often represent only rare individuals or the less numerous larger members of dimorphic populations. In practice, however, nearly all species can be satisfactorily assigned to a single weight class.

Published measurements of body parts (almost always teeth) are often available and these are normally quite sufficient to allow a fossil species to be assigned to a body size class. Although there is argument about exact allometric relationships between body part measurements and body size, it is apparent that there is a sufficiently close relationship to allow

species to be placed within the wide brackets of the size classes used in this study. What must be taken into account, however, is that the relationship varies within taxonomic groups according to major adaptational differences. For instance, the relationship between body size and molar tooth dimensions is different between the microtine and murid rodents whose teeth show quite different morphological patterns (Dreyer, unpublished data). Body size is to some extent related to diet, and as teeth are an intermediate part of this relationship, they might reasonably be expected to covary with both body size and diet.

It was found that, since the weight classes are broad, fossil species could be assigned satisfactorily merely by external examination of the general size of body parts. Blind tests were carried out on modern species from the Palaearctic biota, and fossil specimens from the Pleistocene of Europe and the Eocene of North America. In practically all cases the estimate of body size by examination fell into the same weight class as the estimates based on measurement and published figures for living species. In cases of disagreement, estimates only varied by a single weight class and in all instances this was in the lower end of the weight range (less than 10Kg). No discrepancies were found for the larger body weights.

ii. Diet.

Diet classes:

| | | | |
|---|---|---|---|
| I | Insectivorous | FR | Frugivorous |
| HB | Browsing herbivore | HG | Grazing herbivore |
| CA | Carnivorous | O | Omnivorous |
| HF | Herbivore-frugivore | HI | Herbivore-insectivore |

Sources:

Modern species - Observation of living animals or estimated from tooth morphology.

Fossil species - From tooth morphology and enamel microwear.

The dietary habits of most living forms can be found from the literature (with the exception of very rare species or those known only from museum specimens), but where possible, account was taken of tooth morphology as well, since this is usually the only evidence available for assessing the diets of fossil species. Where the tooth morphology of a living species did not seem to match its recorded diet, the former was stressed more strongly for two reasons. Firstly, this made the method more comparable to that used for fossil forms, and secondly, where the recorded diet is based on a small number of observations of wild individuals, or on observation of captives, it is likely to be an inaccurate reflection of the true dietary habits of the species.

An attempt was made to use a classification based directly on tooth morphology (e.g. the relative importance of enamel crests, cusps and basins, relative size of anterior and posterior dentition) rather than attempting to infer dietary adaptations from morphology, but this was found to be impractical for a number of reasons. Firstly, the resultant system was either so complex, consisting of a large number of morphological classes (many of which were functionally equivalent) that it became cumbersome to use, or so simple that it failed to discriminate between teeth that appeared to show clear functional differences. Secondly, when tooth types were sorted into functionally equivalent classes, these emerged as almost exact replicas of the original dietary classes in terms of the species each contained. It was decided therefore to keep the "dietary" classes but to place as much emphasis as possible on tooth morphology so that the inference of "diet" in modern and fossil species was as comparable as possible.

Each of the dietary classes used has a characteristic morphological pattern associated with it. The descriptions below form only a very rough outline of the modal patterns for each class. The anterior dentition is often used for food selection and preparation while the posterior dentition is used for mastication and it is often the posterior tooth rows that provide the most diagnostic dental characters.

Extreme specialists in these dietary classes often show a tendency towards homodonty of the premolar and molar tooth rows. Other characters that have not been specifically mentioned in this classification are cranial morphology and musculature and the shape and orientation of the tooth rows, both of which can also give useful indications about the diet the animal is adapted to eat.

Insectivores (I) - acutely pointed cusps often linked by sharp enamel crests forming shearing blades.

Frugivores (FR) - teeth tend to be bunodont with relatively low, rounded cusps and wide occlusal basins.

Browsing herbivores (HB) - the most extreme pattern characteristic of leaf-eaters is lophodonty where strong enamel crests link buccal and lingual cusps. The anterior dentitions of some browsing species show adaptations for precise selection of food items.

Grazing herbivores (HG) - teeth are selenodont and hypsodont with large numbers of enamel blades exposed at enamel-dentine junctions by wear which results in an efficient horizontal grinding mechanism. Anterior dentition tends to be adapted for a role as a cropping mechanism.

Carnivores (CA) - teeth with pointed cusps and in the extreme, specialised mechanisms such as mesio-distal shearing blades or adaptations for heavy puncture-crushing of bones. The anterior dentition of many carnivorous species is small and apparently unspecialised.

Omnivores (O) - as a result of their unspecialised diet, omnivores are the hardest dietary category to diagnose in terms of tooth morphology. Teeth often show a complex crown based on a bunodont morphology. Omnivores often seem to display a mixture of characters.

Herbivore-frugivores (HF) - teeth usually show a mixture of lophodonty and broad occlusal basins. Cusps are often rounded but lophodonty is not as marked as in specialised leaf-eaters and occlusal basins are sometimes less broad than in frugivores.

Herbivore-insectivores (HI) - teeth are a cross between HB characters and I characters. Cusps are pointed but not as acute as those of insectivores, occlusal basins are broader than in insecivores, and there is sometimes a tendency towards bucco-lingual lophodonty.

Apart from very rare examples of foodstuffs preserved in stomach contents, coprolites, or trapped between teeth, tooth morphology is the only available evidence for the diet of animals in the fossil record. Unfortunately, tooth morphology does not show directly what the animal ate while it was alive, but merely the kinds of foods its evolutionary history adapted it to eat. This morphology is a compromise between the adaptive pressures exerted mainly through the mechanical properties of the foodstuffs consumed in the evolutionary past, and the inertial effects of developmental processes on the teeth. The result is a functional solution to a mechanical problem, constrained by developmental processes. Tooth morphology does not therefore accurately reflect what an animal actually ate, but rather what kind of food it was adapted to eat. In most cases faunas show sufficient diversity of dietary types that distinctive, habitat related patterns can be observed in practice.

Recently however, it has become evident that the microwear observable on tooth enamel may provide another way of inferring diet. Microwear studies provide a means of indicating the actual diet of an individual specimen, or at least indicating the mechanical properties of the foods consumed during its last few meals before death. Foods having different mechanical properties leave different patterns of fine pits and

scratches on the enamel of teeth (Walker, 1980). It is also possible that because of the differential way in which teeth are used for food preparation and chewing, differences between the microwear on different teeth of a single individual may also indicate import nt dietary characteristics (N. Solounias, pers. comm., 1981). Unfortunately, much basic ground work remains to be done on this technique before it has practical use for dealing with the dietary diversity of whole faunas.

iii. Locomotor specializations.

Locomotor classes:

| | | | |
|---|---|---|---|
| LG | Large ground-adapted | SG | Small ground-adapted |
| AR | Arboreal | S | Scansorial |
| AQ | Aquatic | FO | Fossorial |
| AE | Aerial, flying | | |

Sources:

Modern species - from observation of living animals or examination of morphology.

Fossil species - from examination of skeletal morphology.

In the original conception of Ecological Diversity it was not a species' locomotor adaptations or specializations that were defined so much as the part of the habitat that the animal occupied, particularly for feeding. This information cannot be defined for fossils but locomotor adaptations, which can be inferred from morphology, can give some idea of the area of the habitat that the species was able to use. A certain amount of evidence can be gained from the skull and the axial skeleton, for instance about habitual body posture and robusticity of muscle origins, but the most diagnostic characters are generally found in the appendicular skeleton. These adaptations principally involve two areas, the limb joints and the limb extremities. The joints reflect the degree of stability

or flexibility required during locomotion, while the limb extremities can often be specialized for some particular purpose such as gripping during climbing, or as a "shovel" or "paddle". The locomotor classes used in this study are in many cases associated with a distinctive suite of characters which allow animals to be assigned with acceptable accuracy although clearly this does not allow the detection of species that may facultatively fall into a class other than the one for which they appear to be adapted. Details about locomotor behaviour was taken from the literature in many cases, but as much emphasis as possible was given to morphological evidence and where there was an apparent conflict, benefit was given to morphology rather than recorded observations.

Large ground-adapted (LG) - the limbs of specialist terrestrial animals show adaptations for stability rather than flexibility. Abduction is usually restricted, most movement being in an antero-posterior plane. Some joints may be stabilized by fusion, for instance of the tibia and fibula, which is common in several groups. Limb extremities are also adapted for stability, often involving a reduction in the number of digits and sometimes specialization of the nail to form a hoof.

Small ground-adapted (SG) - usually show some terrestrial adaptations but they are often more generalized in their limb structure than large ground-adapted mammals. This generalized structure, together with their small size enables them to climb facultatively.

Arboreal (AR) - species occupying the branch and small branch zone of the habitat normally possess a limb structure that shows flexibility rather than stability, with a wide range of movement at most joints although hind-limb domination during locomotion may necessitate adaptations for stability in the hind legs. Arboreality also requires some means of efficient attachment to the substrate, often in the form of claws or gripping by the digits.

Scansorial (S) - the limb structure of species which occupy the trunk and large branch zone of the habitat may reflect greater flexibility than that found in small ground-adapted mammals, but more stability than found in specialized arboreal species.

Aquatic (AQ); Fossorial (FO) - swimming and digging mammals tend to be similarly adapted for movement through a substrate that is more dense than air. Skulls frequently have a "streamlined" appearance and limbs are often short and stout being adapted to

perform powerful movements. Limb extremities may also be specialized to function as paddles or shovels.

Aerial (AE) - there are two fundamentally different kinds of aerial mammals, those that fly and those that glide. Flying mammals (the bats) have an extreme and instantly recognisable morphology. The digits of the forelimb are adapted to support a wing membrane and the whole skeleton is generally fragile and adapted for lightness. Gliding animals show few specialized features in their skeletal morphology alone. When not flying these animals often occupy the trunk and large branch zone and their morphology tends to fall into the scansorial class. Because of the difficulty of identifying gliders and the rarity of bats in the fossil record, the aerially adapted class has not been used in any of the analyses presented below.

## 5. Distinctions Between Indicator and Diversity Methods.

Indicator and Diversity methods are the two dominant approaches to the problems of palaeoecological interpretation. For this reason it is very useful to contrast them more directly. The population methods will not be discussed in any detail although in most respects they are most similar to diversity methods. The major distinctions between the different approaches lie in a number of areas:

a. Information required.

b. Methods of inference.

c. Nature of results obtained.

d. Effects of taphonomic bias.

e. Effects of geological age.

### a. Information required.

One of the main differences between indicator methods and diversity methods is in the nature of the information that species are assumed to carry. For indicator methods this information comes from the fossils through either taxonomic identity, morphology and morphological changes, or quantified population characteristics. For diversity methods the information is gathered either directly from individual specimens (evidence of body weight, and dietary and locomotor habits for Ecological and Residual Diversity) or from quantified abundance data (relative minimum number of

individuals for equitability and heterogeneity). For the diversity methods taxonomy is not so important as long as the different species represented in an assemblage are recognised.

One of the objects behind the classification of species for the various methods is to obtain the same information for species in fossil assemblages as that available for those in modern communities. In all cases every effort is made during the classification of modern species to use methods that are similar to those used for fossil forms. This makes the results for modern and fossil species as comparable as possible. Clearly, this is hard to acheive for indicator methods since habitat preference and distribution patterns are characteristics that can only be accurately observed for living populations. Most of the population and diversity methods concentrate on patterns of adaptation that can be identified in a comparable way in both modern and fossil faunas.

Indicator species methods require the classification of modern species according to one of four criteria depending on the method chosen:

i. A single habitat preference; (Traditional Indicators).

ii. Unweighted preference across a predetermined range of habitats; (Habitat Spectra).

iii. Weighted preference across a predetermined range of habitats; (Taxonomic Habitat Index).

iv. Microhabitat preferences; (Biotope Spectra).

Fossil species have to be classified according to the following criteria:

i. Closest living relative or relatives; (Traditional Indicators and Biotope Spectra).

ii. Taxonomic level at which the closest living relative is related; (Taxonomic Habitat Index).

iii. Weighting of the taxonomic level at which the closest living relative is related; (Habitat Spectra).

Population methods require information about modern and fossil populations as follows:

i. Social organization, sex ratio, population structure, sexual dimorphism; (Socioecology).

ii. Mean body mass of species population; (Mean Body Mass).

Diversity methods require information about the species in both modern and fossil communities:

i. Weight, diet and locomotor adaptations; (Ecological and Residual Diversity).

ii Relative abundance of species; (Equitability).

iii. Relative abundance of species and species richness; (Heterogeneity).

b. Methods of Inference.

All of the palaeoecological approaches discussed above use one of two methods of inference which are referred to as inference by identity and inference by structure. The first, inference by identity, is the form used by most of the indicator methods. Since, at its simplest, the argument behind indicator species is that the presence of a particular taxon indicates the presence of a particular habitat type, it is therefore the identity of a species that determines what conclusions are reached. The second method, inference by structure, is the form used by the population and diversity methods. These approaches draw conclusions about the palaeoenvironment on the basis of character states within populations, or patterns and properties of communities in a way that does not regard particular species as being diagnostic.

The reliability of these two methods of inference depends on the soundness of the assumption of ecological uniformitarianism in each case. (Uniformitarianism is the doctrine that subscribes to "the permanency of the laws of Nature" (Lyell, 1830, cited by Vita Finzi, 1973)). As a rule of thumb, where it is possible to identify spatial variation in a character (which can range from morphology and behaviour to population structure and community structure) at the present time, it seems likely that the form of the

character is not so immutable as to preclude the possibility that temporal variation might also exist. If a character is spatially invariable then there is more chance that it will be temporally invariable as well.

Mammals are very adaptable and many species can be found in a range of habitats (see appendix 1). Where the present preferences of many species are so flexible it seems likely that they could have been equally flexible in the past and some species may have occupied different habitats from those in which they are found today. By contrast, there seems to be a strong determinism exerted by habitat types over the ecological diversity of the communities occupying them. For instance, the tropical forests of South-East Asia, Central America, East and West Africa all support communities of similar adaptational structure. In cases such as this where structures are consistently linked with a certain habitat and there are only minor variations over perhaps thousands of miles, it seems that the assumption of uniformitarian principles is relatively safe. This clearly applies to Ecological Diversity, and the same is probably true for Equitability and Heterogeneity, but it is difficult to comment on the population methods since data are only available for relatively few species.

c. Nature of the results obtained.

The different palaeoecological methods can be distinguished by the nature of their results. The basic aim in most cases is to describe the habitat or palaeoenvironment but because Ecological Diversity and Residual Diversity invest each species with less information content than the indicator methods, they inevitably give a less exact description of the environment. However, their apparent theoretical soundness makes this result more reliable than those given by indicator methods.

A distinction must also be drawn between habitat identification and environmental description. Description involves the outlining of various characteristics of a habitat whereas identification involves putting a name to a recognised pattern or habitat type. Descriptive methods are likely to be superior since they can be applied to any habitat type whether modern or extinct. A description of conditions in the habitat can, and often does lead to an identification of the habitat type, whereas simple identification is only useful in that once a habitat has been identified this implies the existence of certain environmental conditions. In some cases this can be misleading since plant associations included in named vegetation types can be quite diverse in certain characteristics. In addition, identifying methods can

only detect known habitat types which in most cases are extant modern habitats. The abilities of the various palaeoecological methods are as follows:

i. Indicator methods.

Traditional Indicators - identify only extant habitats.

Methods weighting variability - identify patterns but patterns can be predicted for non-extant habitats.

Biotope Spectra - describe environmental conditions suiting the biotopic requirements of species.

ii. Population methods.

Socioecology - describes environmental conditions such as dispersion of food resources.

Mean Body Mass - describes conditions such as climatic variations.

iii. Diversity methods.

Equitability and Heterogeneity - describe conditions such as environmental stability and complexity of niche structure.

Ecological and Residual Diversity - describe conditions such as the amount and configuration of available niche space.

d. Effects of Taphonomic Bias.

Methods which require information such as minimum number of individuals, relative abundance, population structure and mean body mass of a population are seriously affected if a fossil assemblage is not representative of the original community or population.

Where the sample is completely unrepresentative the use of these methods is precluded altogether. Methods which can use presence/absence data alone have a much greater immunity to taphonomic effects. Taphonomic biases influence indicator and diversity methods differently and the ways in which some of these methods behave under conditions of species loss are described in detail in chapter 5.

Indicator methods such as Taxonomic Habitat Index, Habitat Spectra and Biotope Spectra, where most or all the fauna is used, are relatively insensitive to species loss, even when this is non-random. Ecological Diversity is sensitive since loss affects the apparent structure of a community and generally Residual Diversity works better the larger the fauna, mainly because larger faunas are more likely to preserve something of the original diversity patterns. In regions that naturally have smaller communities (e.g. temperate regions) Ecological and Residual Diversity are less able to detect significant differences between habitat types. Under these circumstances indicator methods probably hold hope of greater success where their methodological drawbacks may be outweighed by the potential for successful results since it seems that in many cases indicator methods give reasonable results even if they are theoretically questionable.

e. Effects of geological age.

The geological age of an assemblage also affects the working of indicator and diversity methods in different ways. The diversity methods work through inference by structure (as also do the population methods) and there is no particular reason to believe that there has been extensive change in these basic forms of adaptational structure through time. On the basis of this, methods which use inference through structure should be equally effective for faunas of all ages. Indicator species methods work through inference by identity which relies heavily on the relationship between fossil forms and their living relatives in such a way that as the relationship becomes more distant the results become less certain. The effectiveness of indicator species methods is thus reduced with increasing geological age as the average degree of relatedness between the fossils and their extant relatives decreases. When the Taxonomic Habitat Index is used this factor is taken into account as the more inclusive taxa that necessarily have to be used are seen to be less specific in their habitat preferences and the results obtained from assemblages of increasing geological age are automatically less precise.

Chapter 3: Summary.

Chapter 3 discusses and contrasts the theoretical background and practical applications of various palaeoecological methods. Three main approaches for mammalian palaeoecology are discussed, indicator methods, population methods and community diversity methods.

Indicator methods work by allocating habitat preferences to fossil species. These preferences have to be inferred from modern species and the best methods are those that take into account variability in the habitat preferences of modern species and variations in the closeness of the relationship between modern and fossil species. Traditional indicators do not do this, but three of the described methods do: Taxonomic Habitat Index and Habitat Spectra, both of which weight variability numerically, and Biotope Spectra, a method which uses microhabitat preferences.

A number of possible ways of using population methods are suggested, but these are not examined in any depth.

Diversity methods use the responses of higher level ecological units, such as communities, as the means of studying palaeoenvironments. A number of methods are described of which two, Ecological Diversity and Residual Diversity, are examined in detail. The latter method, Residual Diversity, is specifically designed to be able to take into account taphonomic biases introduced during fossilization.

Finally, indicator and diversity methods are contrasted in terms of the information each requires, the method of inference used, the nature of the results obtained and the effects of taphonomic bias and geological age.

# Chapter 4

## Modern habitats and communities

1. Introduction.

The aim of palaeoecological analysis is environmental reconstruction and in the first instance this usually means discovery of the habitat or vegetation type inhabited by a fossil fauna. Once the vegetation type is known, this implicitly conveys all sorts of other pieces of information about the environment. A complete review of all modern habitats could not possibly be given here: The aim of this chapter is to give an outline of the main climatic climaxes and to describe some of the characteristics of these habitats that are important influences on the distribution of species and the structure of communities. The distributions of individual species are controlled by tolerances to all kinds of variables; characteristics of the vegetational habitat are sometimes, but not always, of direct importance as limiting factors. Work by Andrews et al. (1979), Fleming (1973), Cody (1966; 1975), Harrison (1962) and Nel (1975) suggests that community structure is intimately linked with habitat type. The model of Ecological Diversity described in chapter 3 is formulated in such a way that differences between communities are interpreted as resulting from differences in the amount and configuration of niche space available in the habitat. Important determinants of this habitat niche space include the structure and the physical complexity of the habitat, productivity, the availability of edible resources, seasonality and stability.

a. Habitat Structure and Complexity.

Structure and physical complexity partly control the extent to which ecologically similar species can avoid competition. The more physically complex the environment, the more opportunity it provides for potential competitors to avoid each other by occupying spatially different parts of the habitat. There are several important facets to habitat structure, one of which is the nature of the substrate. For instance, soil conditions can be of considerable significance: Dry and light textured soils favour the activities of digging and burrowing species, whereas compact, waterlogged, lateritic and permanently frozen substrates all discourage digging. Discontinuity or absence of the ground surface in some habitats, such as swamps, may result in the absence of practically all terrestrially adapted species.

A second important feature is the structure of the plant community; on the one hand the size and shape of individual plants and on the other, the way in which these combine to form higher order structures such as continuous branch layers and canopies of foliage. The least complex habitats are those that consist of a vegetation monolayer at ground level such as tundra and grassland. The most complex structures consist of a number of strata of branches and foliage at varying heights above the ground. This kind of structure is found in mature forests, typically in tropical regions.

The structure of a habitat can be described in a very simple way by the spectrum of growth-forms found among its constituent species (Raunkaier, 1934; Whittaker, 1970). One character of plant growth-form is the position of the perennating tissues relative to the ground surface. Perennating tissues are the parts of a plant that remain active during a winter or dry season and then resume growth with the return of favourable conditions (Whittaker, 1970). Since these tissues are so vital to the survival of the plant, their position is an important feature of the plant's adaptations.
In general, the harsher the climate, the fewer species are likely to have buds far above the ground surface where they are more exposed to cold and desiccation than buds nearer the ground. Raunkaier (1934) used the position of the perennating tissues to define five main types of land plants:

i. Phanerophytes - woody plants with buds well above the ground surface, fully exposed to the atmosphere. This class includes trees and shrubs down to an arbitrary minimum height of 25cm. (Whittaker, 1970).

ii. Chamaephytes - plants whose perennating tissues are borne between the ground surface and a height of 25cm. where they are less exposed than those of Phanerophytes. Chamaephytes include dwarf shrubs, semi-shrubs and small succulents.

iii. Hemicryptophytes - perennial herbs with buds at the ground surface where additional protection may be gained from leaf litter and snow.

iv. Geophytes - perennial herbs with underground perennating tissues such as bulbs, corms, rhizomes and tubers. The buds of this life form are almost entirely protected from the above-ground climate.

v. Therophytes - annual or ephemeral herbs which survive unfavorable seasons or longer lengths of time as seeds.

The relative abundance of these life-forms among the plants of a community not only indicates something about the probable climatic influences, but also describes the physical structure of the community in a very simple way, at least in terms of plant height. Certain life-forms are usually dominant or most conspicuous in a community and table 4.1 gives the life-form spectra of some of the main habitat types described below. Raunkaier (1934) provides an extensive comparison of many habitat types using the same kind of spectra.

Table 4.1. Life-form spectra of major habitat types.

| Habitat type | Phanero-phytes | Chamae-phytes | Hemicrypto-phytes | Geo-phytes | Thero-phytes |
|---|---|---|---|---|---|
| Tropical rainforest | 96 | 2 | - | 2 | - |
| Subtropical rainforest | 65 | 17 | 2 | 5 | 2 |
| Warm temperate forest | 54 | 9 | 24 | 9 | 4 |
| Cold temperate forest | 10 | 17 | 54 | 12 | 7 |
| Tundra | 1 | 22 | 60 | 15 | 2 |
| Dry grassland | 1 | 12 | 63 | 10 | 14 |
| Semidesert | - | 59 | 14 | - | 27 |
| Desert | - | 4 | 17 | 6 | 73 |

b. Productivity.

Plant matter is the primary resource for all vertebrate food chains and the primary productivity of a habitat is an important feature because, in simple terms, the greater the productivity, the more extensive and varied the food chains that can be supported. Plant matter is eaten by primary consumers who are preyed upon by secondary consumers, who in turn fall victim to tertiary consumers and so on. The more productive the habitat, the greater the richness of primary consumers, which will in turn be reflected by the richness of consumers at higher levels. The overall effect is for more productive habitats to support richer communities than less productive habitats.

It is necessary to distinguish between Net Primary Productivity (N.P.P.) and Gross Primary Productivity (G.P.P.). The latter is the amount of chemical energy fixed by photosynthesis (which is usually expressed for a given unit of land area over a given unit of time). Net Primary Productivity represents Gross Primary Productivity less the energy lost through plant respiration and is equivalent to the chemical energy stored per unit area per unit time (Barbour et al., 1980; Odum, 1971). The resources available for exploitation by a mammal community are a function of N.P.P.. The higher the N.P.P., the higher the potential of the habitat to support primary

consumers (provided that the productivity is in a form that can be exploited by the consumers). Higher productivity generally supports a greater biomass of consumers and there seems to be a tendency for increased productivity to result in increased species richness as well. This is particularly true in habitats where high productivity is accompanied by a varied range of resources which allows species to avoid competition by efficient resource partitioning. Table 4.2 gives the Net Primary Productivity for some of the major habitat types discussed later in the chapter.

Table 4.2. Net primary productivity of major habitat types.

| Habitat type | Normal range ($gm/m^2/yr$) | Mean |
|---|---|---|
| Tropical rainforest | 1000 - 3500 | 2200 |
| Tropical seasonal forest | 1000 - 2500 | 1600 |
| Deciduous forest | 600 - 2500 | 1200 |
| Boreal forest | 400 - 2000 | 800 |
| Tundra and alpine | 10 - 400 | 140 |
| Steppe | 200 - 1500 | 600 |
| Savannah | 200 - 2000 | 900 |
| Semidesert and desert | 10 - 250 | 90 |

c. Stability.

Instability in the environment may make the habitat periodically unsuitable for occupation by some of the species in a community. Seasonal patterns of instability (seasonality) can sometimes require long-term inhabitants of a habitat to find some means of coping with less favorable seasons if their presence from year to year is to be guaranteed. Species present in habitats where seasonality is an important consideration can be affected by variations in the carrying capacity of the habitat, or directly by climatic factors. The richness of the species that are resident and active throughout the year is determined principally by the carrying capacity during the least productive season. Some species may overcome the problems of diminished carrying capacity and harsh climate either by becoming torpid (hibernation and aestivation) or by migrating to areas where survival is less difficult. This problem hardly arises in the tropics but at higher latitudes it becomes increasingly significant. One of the basic environmental differences between the tropical and temperate regions is that low temperatures and frosts, which conform to a seasonal pattern in extra-tropical latitudes, are relatively unimportant in the tropics where seasonality is usually related to periodic water deficiency rather than fluctuations in temperature (Walter, 1973).
Another basic difference is found in the intensity and

length of daytime insolation. In temperate regions sufficient insolation for plant growth is received during only part of the year (the growing season), whereas in the tropics daylength and intensity of solar radiation favour growth throughout the year. The length of the growing season thus varies with latitude and increases as latitude decreases.

All the vegetation types described below are "climatic climaxes", which means that they are potentially stable and are likely to persist in an area over long periods of time. These habitat types are considered to have reached an equilibrium state, but any instability in the habitat covering an area over a period of time can seriously affect the mammal community living there. Catastrophic instability can periodically change the environment to such an extent that many species may be unable to survive the altered conditions. Habitats that have suffered this kind of instability will often be inhabited by impoverished communities. The pattern of this kind of depletion is hard to predict although species which appear after catastrophic events are likely to be generalists that can adapt to changed conditions and r-selected species whose reproductive abilities suit them to the colonization of secondary and unstable habitats. A detailed exploration of this question with particular reference to the colonization by bird species of islands in New Guinea is to be found in Diamond (1975).

A third aspect of instability in natural habitats is presented by successional events. Succession and climatic climaxes are dealt with in the next section.

d. The Climatic Climax Concept.

Habitat types do not simply appear complete. They develop through a process known as succession which is a directional cumulative change through time in the species occupying a given area (Barbour et al., 1980). The final stage of this progression is a stable state known as the climax community. This stability implies an equilibrium state with the prevailing conditions and although changes do occur in climax communities, they are not directional and cumulative, so that they tend merely to result in a fluctuation round some long term mean. For a given region it is convenient, although often rather arbitrary, to recognise a single climatic climax which is in equilibrium with the general climate, edaphic climaxes which are modified by local conditions of the substrate and a number of successional or "seral" communities which are undergoing the gradual cumulative change that eventually results in the mature climax. The climax is the community towards which all successional development is tending in a given region, "which is acheived where local conditions are not so extreme as to seriously modify the effects of the regional climate" (Odum, 1971). Local conditions such

as topography, soil type, water, fire or other disturbance are all factors that prevent the climatic climax from developing, but the primary limiting factors are as follows:

i. The availability of water (amount and distribution of annual rainfall, evaporation effects, and the relation between these two factors).

ii. Temperature (annual mean, annual range and the relation of these to rainfall patterns).

iii. Light (intensity and the seasonality of daylength).

It is important to distinguish between climax and seral communities for two reasons. Firstly, climax communities are stable through long periods of time (measured on an ecological or geological scale) whereas seres can only be considered stable over short periods. Consequently, while climax plant communities support potentially stable mammal communities, seres do not. Secondly, edaphic climaxes and seral plant communities are modified by all sorts of influences, many of which are of short duration (in ecological or geological terms) or locally derived and while the true climax of a given region can often be predicted from patterns of regional climate, the prediction of seres is not so straightforward.

In the rest of this chapter climax habitats from the tropics and from temperate regions of the northern hemisphere are discussed. Subtropical habitats are not dealt with since none of the case studies presented in later chapters relate to subtropical areas.
The structure of mammal communities from subtropical habitats and the palaeoecology of faunas that appear to originate from formerly subtropical regions are also the subject of current research (Artemiou, in prep).

None of the climaxes described below are completely homogeneous. All show variation in species composition, physical structure and ecophysiology from area to area and the descriptions that are given are only general outlines of these habitat types in terms of some of the factors that may be of significance to the mammal communities inhabiting them. Many sources have been used and more detailed information is available particularly concerning species composition (Money, 1965; Eyre, 1968; Walter, 1973), ecophysiology (Walter, 1973) and soils (Eyre, 1968; Money, 1965).

e. Mammal Communities.

i. Methods of compiling faunal lists.

Faunal lists for modern communities can be compiled from two sources, either from published and unpublished records of field studies and collections made in the field, or alternatively from distribution maps, but these two methods imply two quite different concepts of the community. Records of field studies and collections made in areas of a single known habitat type are records of the animals actually living together in an "ecological" community. On the other hand, a list compiled from distribution maps represents a "geographical" community composed of all species whose ranges of distribution overlap at a chosen point on the map. There are some distinctions between these types of community: An ecological community can be associated with any habitat type whether it is seral or climax, whereas the geographical community is only a notional community and the habitat with which it has to be associated is the notional habitat at the same point on the map, which in practice is normally the climatic climax for the area. There is often little evidence about whether or not all the species whose distributions cover a particular point on the map can actually be found together in a single ecological community. Species may be associated with different stages of successions leading to the climax and minor differences

in microhabitat preferences can result in some species never being found in the same ecological community, even though they form part of the same geographical community. For this reason and also because some species may escape detection in field samples, there is always the likelihood that an ecological community will contain less species than the geographical community associated with the same habitat.

Although the geographical community is not in every sense a real community, it represents the pool of species present in any given area and ecological communities can thus be regarded as samples drawn from geographical communities. The adaptive structure of an ecological community is taken to reflect the niche space available in a habitat. Provided that it can be shown that geographical communities from a given habitat show consistent patterns of ecological diversity and that these patterns are similar to those of ecological communities from the same habitat type, then it is acceptable to use geographical communities as part of the modern sample.

An example of the similarity of the two types of community is given by a comparison among a series of faunal lists compiled for tundra habitats. This comparison is between 8 lists compiled from distribution maps and 6 from field studies and

collections. Further details about these communities are given on page 249. Tables 4.15 and 4.16 (pp.251 & 253) summarize the ranges and means of the number of species and the proportion of the total communities falling in each class of the Ecological Diversity distribution for the two types of community. Figures 4.16 and 4.17 show the mean values for each type of community plotted as Ecological Diversity histograms. These figures indicate that both community types share similar patterns of adaptive structure and the interpretation of this pattern is discussed in more detail below (see pp. 249-250).

The individual communities can also be compared by looking at their Residual Diversity patterns (figures 4.1 and 4.2). Since ecological communities are considered to be derived from geographical communities, Residual Diversity can show how closely related are the two types of community. This comparison in some respects anticipates the simulations of species loss presented in chapter 5 and the patterns shown here should also be compared with the series of simulations based on a tundra community shown in figures 5.49 and 5.50. Analysis of Residual Diversity also suggests that geographical and ecological communities from tundra areas are closely related. All share the same basic pattern consisting of the irregular polygon enclosing the comparative group of tundra communities (white)

Figure 4.1. Residual diversity of 8 geographical communities from tundra habitats.

The residual diversity patterns of the following geographical communities from tundra habitats are shown (see table 4.3 and Appendix 2):

a. MO/PA/001
b. MO/PA/002
c. MO/PA/003
d. MO/PA/004
e. MO/PA/006
f. MO/PA/007
g. MO/PA/008
h. MO/PA/009

This figure should be compared with the patterns shown in figure 4.2. A key to the interpretation of Residual Diversity patterns is given on page 179 and at Appendix 5.

Figure 4.1.

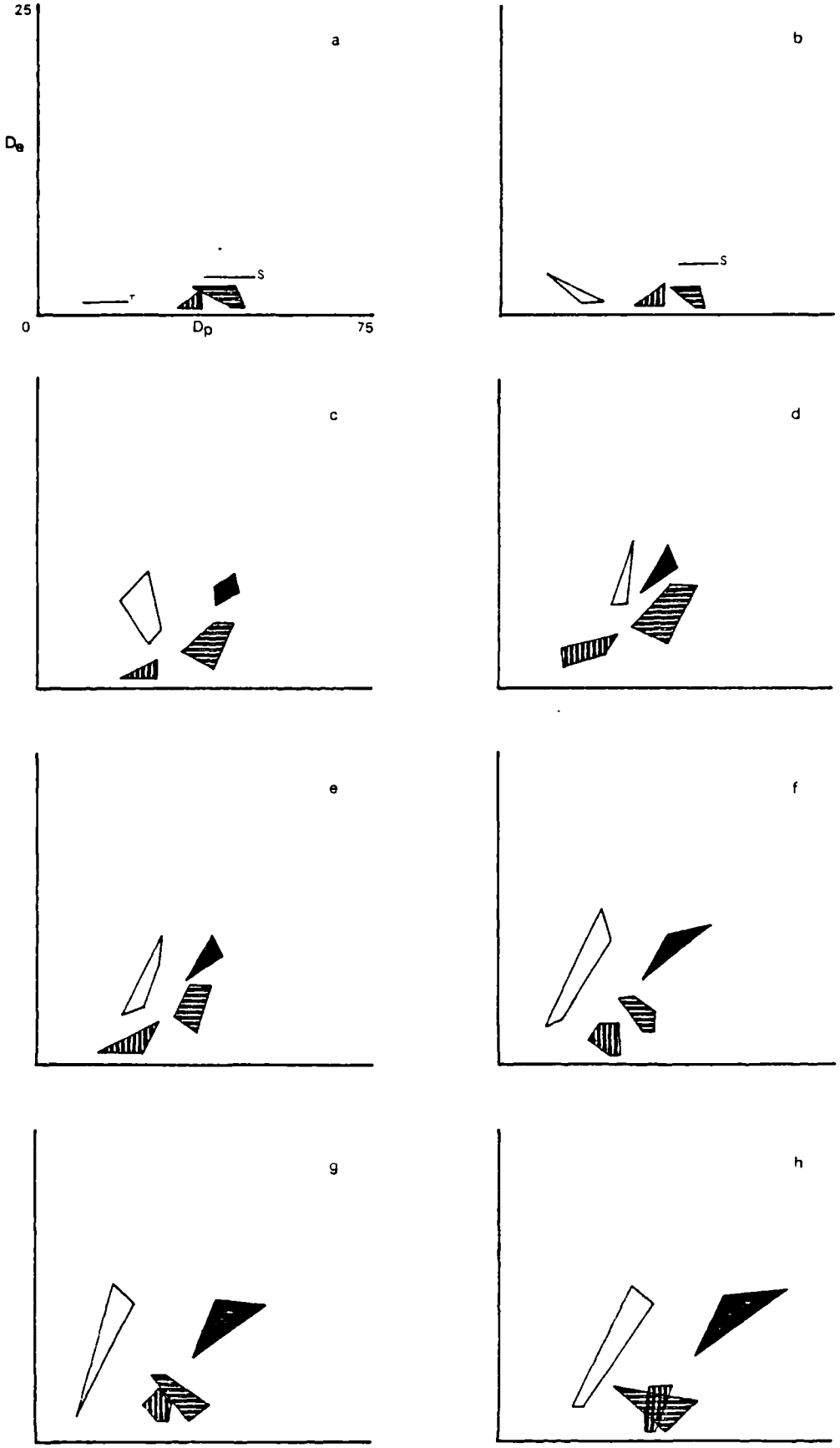


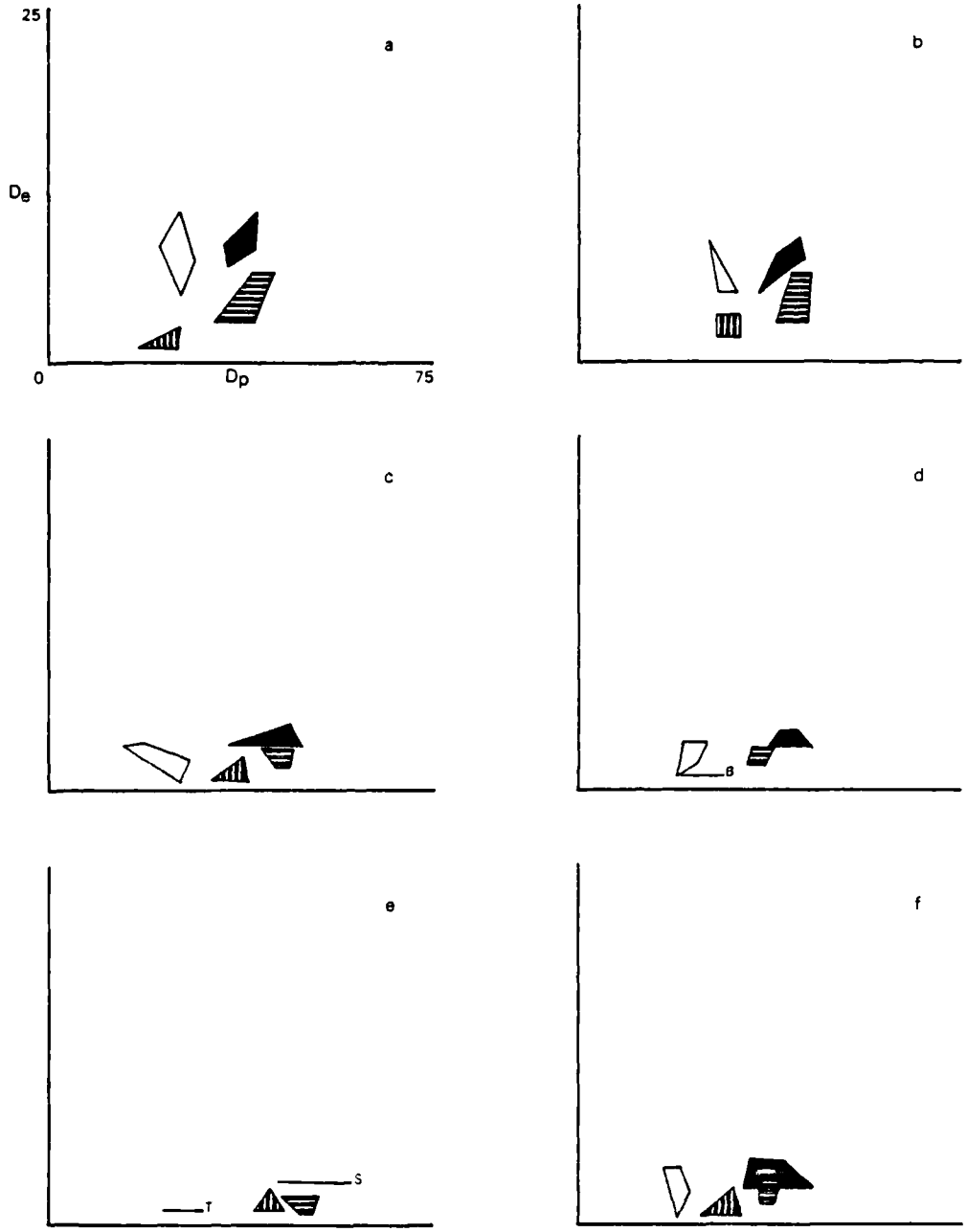
Figure 4.2. Residual diversity of 6 ecological communities from tundra habitats.

The residual diversity patterns of the following ecological communities from tundra habitats are shown:

a. MO/PA/059
b. MO/PA/060
c. MO/PA/056
d. MO/PA/052
e. MO/PA/053
f. MO/PA/054

Comparison of this figure with the patterns shown in figure 4.1 suggests that ecological and geographical communities from tundra habitats and tundra climax zones share similar residual diversity patterns in which the tundra group of communities (white) either lies nearest the origin (as in pattern 4.2c) or lies above the boreal group (as in patterns 4.2a and 4.2b). The deciduous forest group and the semidesert group generally share similar Dp values and lie further from the origin. The patterns in figures 4.1 and 4.2 should also be compared with the simulations based on tundra community MO/PA/009 shown in figures 5.49 and 5.50. A more detailed interpretation of the residual diversity pattern for the same community is given on page 365.

Figure 4.2.



nearest the origin, the boreal and deciduous forest groups (striped vertical blue and horizontal green respectively) to the right of the tundra group, usually close together or even overlapping and the semidesert group (red) to the right of the forest groups, farthest from the origin. These relationships remain comparatively constant and the variations that can be observed result almost entirely from differences in size between the communities rather than gross differences in ecological structure.

A comparison of the Taxonomic Habitat Index patterns of the same communities is presented in figure 4.3. Once again it can be observed that ecological and geographical communities present a similar range of patterns, suggesting a close relationship between the two types of community for tundra habitats.

A similar comparison of communities from temperate deciduous forest is shown in figures 4.4 and 4.5. The Residual Diversity patterns for these communities are similar, although the effect of size differences is more marked than in tundra communities. These figures should also be compared with figures 5.45 and 5.46 in chapter 5. The Taxonomic Habitat Index also indicates that both types of community are very similar.

Figure 4.3. Comparison of THI patterns of geographical and ecological tundra communities.

The THI patterns of the following communities are shown:

| | |
|---|---|
| a. MO/PA/001 | b. MO/PA/002 |
| c. MO/PA/003 | d. MO/PA/004 |
| e. MO/PA/006 | f. MO/PA/007 |
| g. MO/PA/008 | h. MO/PA/009 |
| i. MO/PA/059 | j. MO/PA/060 |
| k. MO/PA/056 | l. MO/PA/052 |
| m. MO/PA/053 | n. MO/PA/054 |

This comparison is between the same 8 geographical and 6 ecological tundra communities whose residual diversity patterns were shown in figures 4.1 and 4.2. The profiles shown here suggest that geographical and ecological communities also tend to share similar THI patterns. It should be noted that although the boreal forest column (B) contains the highest value in many cases, tundra profiles are always distinguished by the high value in the tundra column. This pattern receives more detailed discussion on pages 303 and 489.

Figure 4.3.

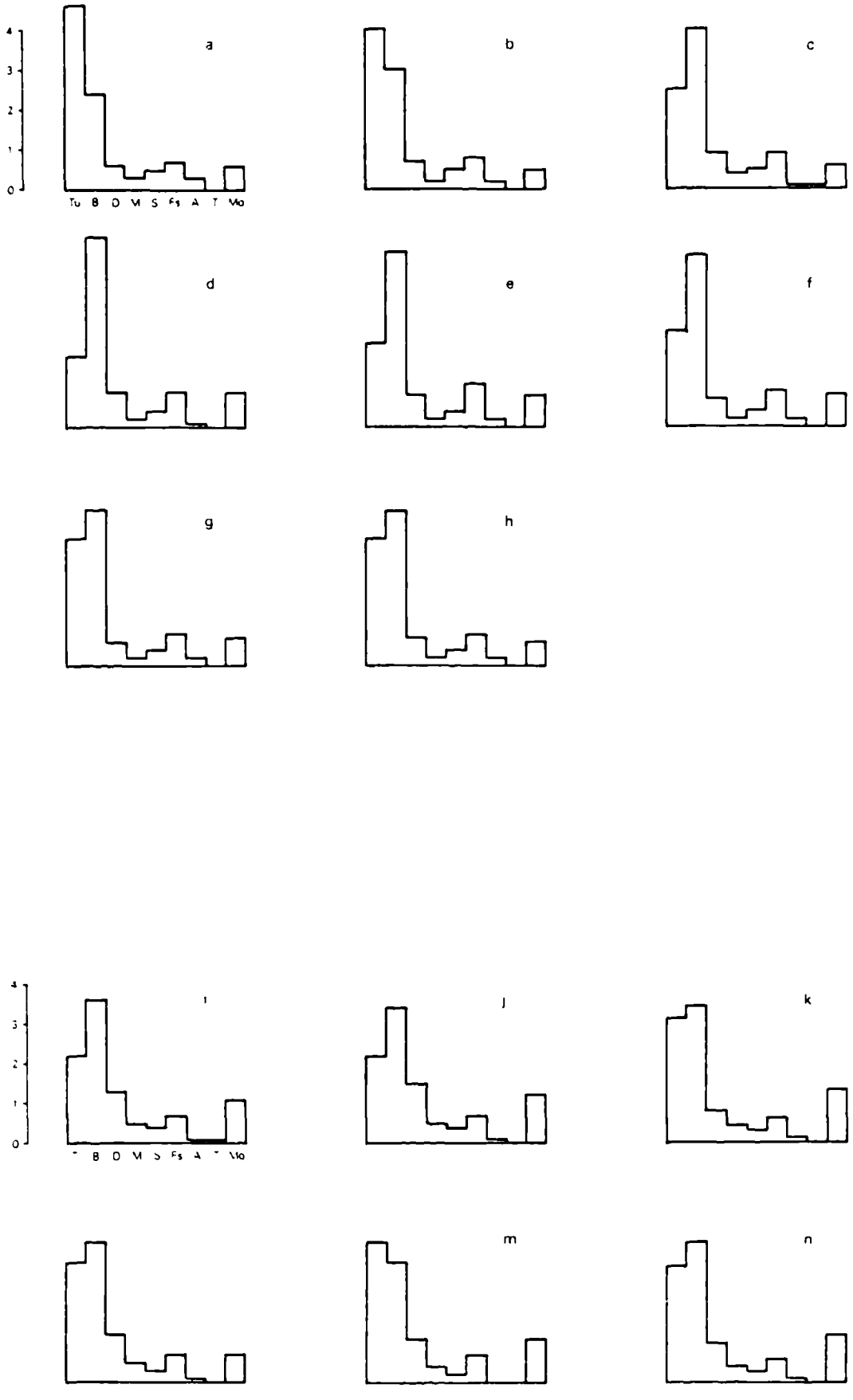


Figure 4.4. Comparison of residual diversity patterns of geographical and ecological communities from deciduous forest.

This comparison shows that geographical and ecological communities from deciduous forest climax zones and habitats share similarities in ecological structure. Although the patterns for the two ecological communities show the four habitat groups in similar relative positions, the patterns appear to be vertically collapsed, which may suggest that the ecological communities are impoverished in comparison with geographical communities from the same habitat.

The interpretation of this residual diversity pattern is discussed in more detail on page 363 and the patterns should also be compared with the residual diversity simulations based on a deciudous forest community illustrated in figures 5.45 and 5.46.

The communities figured are as follows:

Geographical communities:

a. MO/PA/023 b. MO/PA/024

c. MO/PA/025

Ecological communities:

d. MO/PA/057 e. MO/PA/058

Figure 4.4.

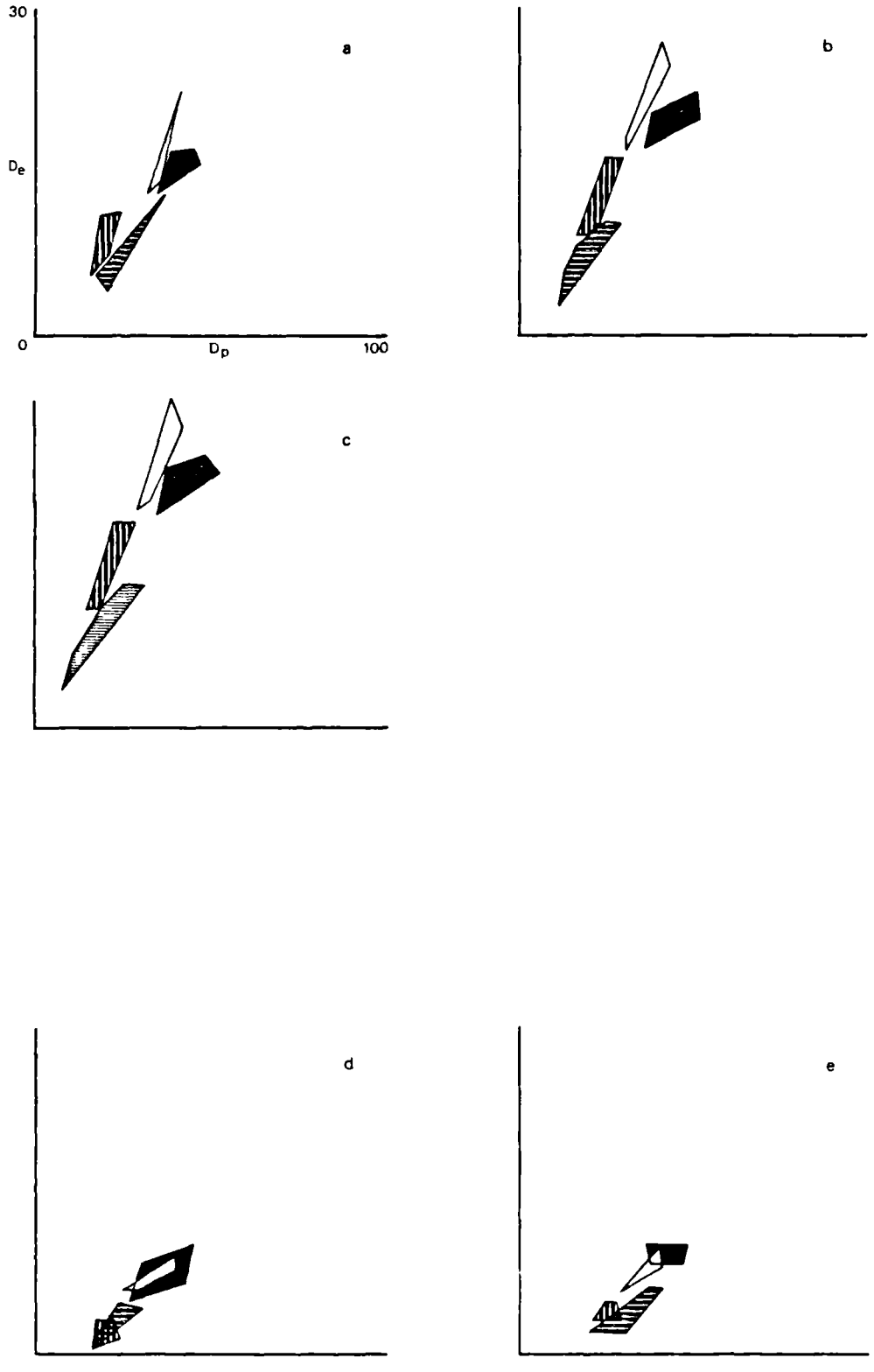


Figure 4.5. Comparison of THI patterns of geographical and ecological communities from deciduous forest.

This comparison is between the same deciduous forest communities whose residual diversity patterns were illustrated in figure 4.4. The profiles shown here suggests that these ecological and geographical communities also share similar THI patterns in which the deciduous forest column (D) dominates over all the others in value.

The communities figured are as follows:

Geographical communities:

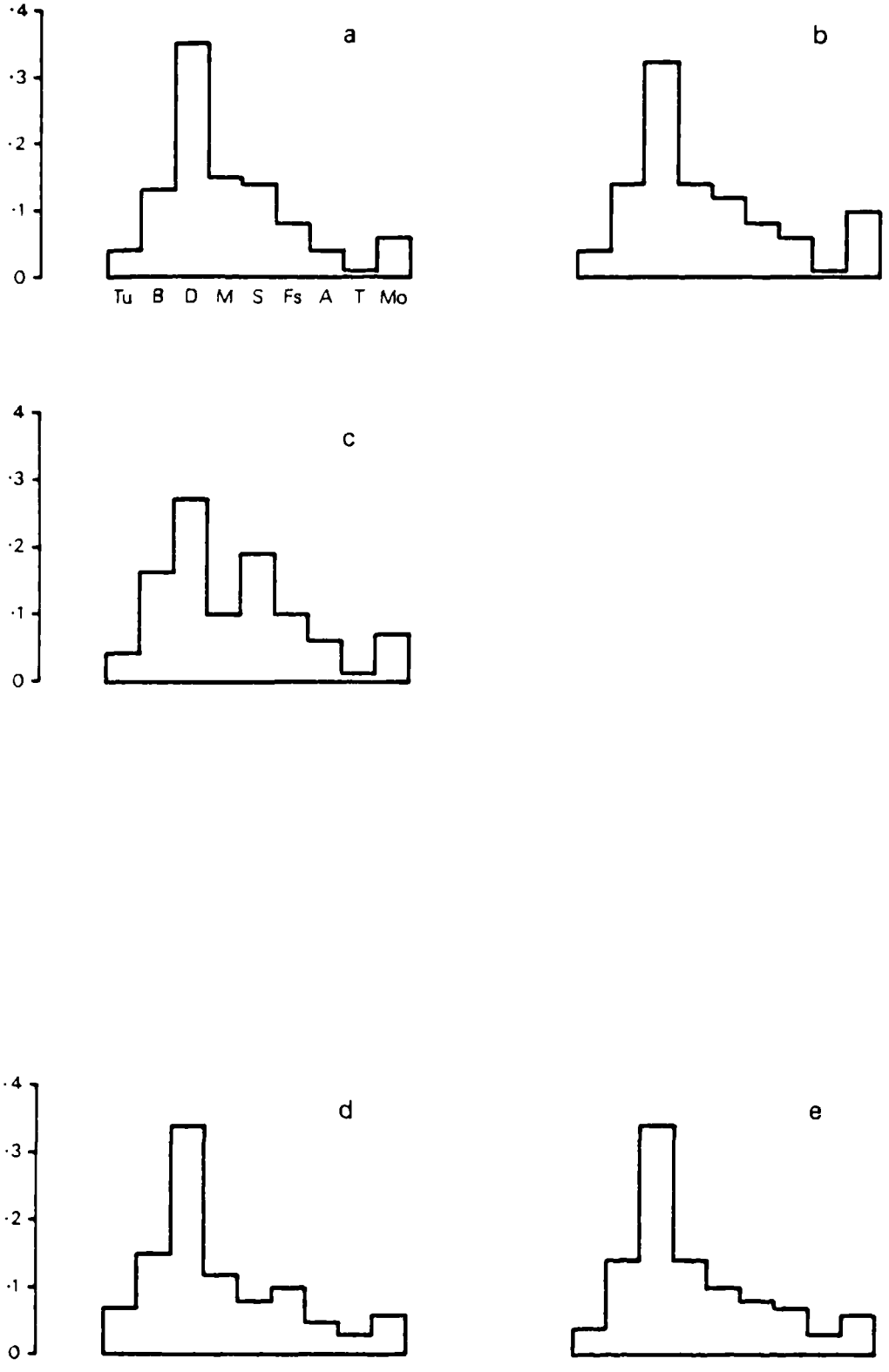
a. MO/PA/023 b. MO/PA/024

c. MO/PA/025

Ecological communities:

d. MO/PA/057 e. MO/PA/058

Figure 4.5.



Ideally this kind of test should be carried out for all habitats, unfortunately the paucity of ecological communities for most Palaearctic habitats means that the majority of the modern comparative sample must perforce consist of geographical communities.

The use of communities compiled from distribution maps can also be justified when the relationship between a living community and a death assemblage, or fossil fauna, is taken into consideration. A fossil fauna can potentially include any species living within the catchment area of the fossil site, which means that any species whose area of distribution overlaps the sedimentary catchment at some time during the formation of the death assemblage could eventually find its way into the fossil fauna. This suggests that in principle, fossil assemblages are more closely related to geographical communities than to ecological communities. Although fossil assemblages and ecological communities may both be regarded as samples drawn from a geographical community, there is no reason to believe that all or even most fossil assemblages are derived from ecological communities. Comparisons with ecological communities may be preferable from a theoretical point of view because they can be more precisely associated with known habitat types, but comparison with geographical communities can be justified on the grounds that these are a better

analogue for the communities from which most fossil faunas are derived. This is another area in which taphonomy can provide a great deal of illumination and taphonomic studies might be particularly pertinent in areas where migration is a common behaviour pattern which seasonally alters the structure of ecological communities.

ii. Ecological diversity of modern communities.

An outline is given below of the ecological diversity of the mammal communities associated with each of the habitats described. The Residual Diversity and Taxonomic Habitat Index patterns for a community from each of these habitats are given in chapter 5 and the Ecological Diversity, Residual Diversity and Taxonomic Habitat Index patterns for all the communities in the modern comparative sets are figured in appendices 1 and 2.

The ecological diversity of a community can be related to characteristics of the habitat in which it lives and the overall pattern can relay information about stability, physical structure and zonation, productivity, diversity of resources and the stability of the seasonal resource base.

Body size has wide-ranging ecological and physiological implications. All communities have more

small-bodied than large-bodied species. The theory of r and K selection indicates that large-bodied species are likely to be more common in stable environments and the energy requirements of a viable breeding population are such that species of large body mass are likely to be more abundant in the more productive environments. Thus, one of the most important features of the weight distribution of a complete community is the number of large-bodied species and their abundance relative to species of a lesser body weight. Body size is also linked with dietary and locomotor specializations: Metabolic constaints require small-bodied species to eat foodstuffs such as fruits, grains, insects, gums and nectar, which all have a relatively high energy content, while larger species can survive by eating foods such as plant foliage which have a relatively low energy yield. The constraints of physical size usually restrict large-bodied forms to terrestrial habits while species occupying trunk and canopy zones are rarely found among the largest size classes. Thus, while the weight distribution and the overall species richness of a community can tell something about the stability and productivity of the habitat, the distribution is also influenced by the relative importance of high and low energy yielding food sources, the physical structure and the productivity of different areas within the habitat.

The relative importance of different dietary types gives an indication of the nature of the available resource base such that an abundance of species in any dietary class suggests an abundance of a particular resource type. It should be realised that the absence of species belonging to a given dietary class does not necessarily imply complete absence of the food on which this class relies; it may be that the food is only seasonally available and thus unsuitable as a base for full-time specialists. Consequently, the dietary adaptations to be found in a community are controlled not only by what resources are available but also by how often and for how long they are present.

The distribution of locomotor types indicates what physical zones are available in the habitat. Habitats where trees are the dominant life-form will support many more arboreal and scansorial species than those where there are few or no trees. However, this pattern is also linked to diet and the availability of resources within a particular zone which puts a potential limit on the number of species that can be supported in that zone. It is likely that two habitats of similar physical structure and equal physical complexity will show different distributions of locomotor adaptations if the productivity of the different zones varies between the habitats.

It can be seen that the controls and limits on the adaptive structure of communities are very complex, however, even at the most general level, Ecological Diversity provides some information about various characteristics of the habitat. The complexity and distinctiveness of natural habitats and the complexity of the relationship with the mammal community means that most habitats support communities with distinctive adaptational structures. In the first instance this means that the habitat can usually be identified and under some circumstances it may also be possible to provide a more complete description of the environment. Unfortunately, the usefulness of Ecological Diversity as a descriptive tool is severely limited if the complete community is not represented.

iii. Modern comparative sets.

In order to make the comparison of fossil faunas and modern communities more manageable in practice, the number of modern communities used in comparisons was restricted. Table 4.3 lists all the modern communities that have been used in this study with their geographical origin, community type and habitat type. Communities forming part of the modern comparative sets are marked "*". These communities have been divided into two sets: African tropical communities and Palaearctic communities, both of which are discussed in more detail below (see pages 224 and 273).

Table 4.3. List of modern comparative communities.

i. Tropical ecological communities.

| Reference | Habitat | N | Location |
|---|---|---|---|
| MO/AF/001* | Lowland evergreen forest | 76 | Zaire |
| MO/AF/002* | Floodplain | 48 | Zambia |
| MO/AF/003* | Montane forest | 64 | Kenya |
| MO/AF/004* | Woodland | 57 | Tanzania |
| MO/AF/005* | Grassland | 41 | Tanzania |
| MO/AF/006* | Woodland | 74 | Tanzania |
| MO/AF/007* | Seasonal forest | 60 | Tanzania |
| MO/AF/008* | Floodplain | 51 | Tanzania |
| MO/AF/009* | Seasonal forest | 61 | Kenya |
| MO/AF/010* | Floodplain/forest | 52 | Kenya |
| MO/AF/011* | Bushland | 72 | Uganda |
| MO/AF/012* | Lowland evergreen forest | 75 | Guinea |
| MO/AF/013* | Woodland | 48 | Rwanda |
| MO/AF/014* | Bushland | 63 | Kenya |
| MO/AF/015 | Woodland | 38 | Sudan |
| MO/AF/016* | Bushland | 66 | Kenya |
| MO/AF/017* | Seasonal forest | 62 | Kenya |
| MO/AF/018* | Seasonal forest | 67 | Uganda |
| MO/AF/019* | Seasonal forest | 57 | Uganda |
| MO/AF/020* | Bushland | 54 | Uganda |
| MO/AF/021* | Seasonal forest | 73 | Uganda |
| MO/AF/022* | Montane forest | 55 | Uganda |
| MO/AF/023* | Montane forest | 64 | Zaire |
| MO/AS/001 | Evergreen forest | 51 | Sarawak |
| MO/NA/001 | Tropical forest | 40 | Balbao |
| MO/NA/002 | Tropical forest | 39 | Cristobal |

Notes: African communities (prefix MO/AF) are all from Andrews et al. (1979) and references cited there (table 1); the South-east Asian community (MO/AS) is from Hanbury Tenison (1980); the two Central American communities (MO/NA) are from Fleming (1973).

Table 4.3. continued. ii. Temperate geographical communities.

| Reference | Climax habitat | N | Location |
|---|---|---|---|
| MO/PA/001* | Tundra | 13 | 70°N 70°E |
| MO/PA/002* | Tundra | 15 | 70°N 80°E |
| MO/PA/003 | Tundra | 22 | 70°N 90°E |
| MO/PA/004 | Tundra | 27 | 70°N 100°E |
| MO/PA/005 | Tundra | 24 | 70°N 110°E |
| MO/PA/006 | Tundra | 25 | 70°N 120°E |
| MO/PA/007* | Tundra | 26 | 70°N 130°E |
| MO/PA/008* | Tundra | 25 | 70°N 140°E |
| MO/PA/009 | Tundra | 23 | 70°N 150°E |
| MO/PA/010 | Boreal forest | 31 | 60°N 10°E |
| MO/PA/011* | Boreal forest | 41 | 60°N 40°E |
| MO/PA/012* | Boreal forest | 44 | 60°N 50°E |
| MO/PA/013* | Boreal forest/montane | 43 | 60°N 60°E |
| MO/PA/014 | Boreal forest | 37 | 60°N 70°E |
| MO/PA/015 | Boreal forest | 36 | 60°N 80°E |
| MO/PA/016 | Boreal forest | 35 | 60°N 90°E |
| MO/PA/017* | Boreal forest | 32 | 60°N 100°E |
| MO/PA/018* | Boreal forest | 31 | 60°N 110°E |
| MO/PA/019* | Boreal forest | 32 | 60°N 120°E |
| MO/PA/020 | Boreal forest | 28 | 60°N 130°E |
| MO/PA/021 | Montane | 22 | 60°N 140°E |
| MO/PA/022 | Boreal forest | 26 | 60°N 150°E |
| MO/PA/023* | Deciduous forest | 43 | 50°N 10°E |
| MO/PA/024* | Deciduous forest | 46 | 50°N 20°E |
| MO/PA/025* | Deciduous forest | 51 | 50°N 30°E |
| MO/PA/026* | Steppe/forest-steppe | 47 | 50°N 40°E |
| MO/PA/027 | Steppe/semidesert | 35 | 50°N 50°E |
| MO/PA/028* | Steppe | 39 | 50°N 60°E |
| MO/PA/029* | Steppe | 36 | 50°N 70°E |
| MO/PA/030 | Steppe | 43 | 50°N 80°E |
| MO/PA/031 | Montane | 65 | 50°N 90°E |
| MO/PA/032 | Montane/forest-steppe | 48 | 50°N 100°E |
| MO/PA/033 | Boreal forest | 49 | 50°N 110°E |
| MO/PA/034 | Steppe | 42 | 50°N 120°E |

Table 4.3. continued. Temperate geographical communities continued.

| Reference | Climax habitat | N | Location |
|---|---|---|---|
| MO/PA/035 | Boreal forest | 44 | 50°N 130°E |
| MO/PA/036 | Boreal forest | 38 | 50°N 140°E |
| MO/PA/037 | Mediterranean | 24 | 40°N 0°E |
| MO/PA/038 | Mediterranean | 33 | 40°N 20°E |
| MO/PA/039 | Mediterranean/steppe | 40 | 40°N 30°E |
| MO/PA/040 | High steppe | 49 | 40°N 40°E |
| MO/PA/041 | Boreal/mixed forest | 48 | 60°N 30°E |
| MO/PA/042* | Semidesert | 26 | 40°N 60°E |
| MO/PA/043 | Steppe/semidesert | 38 | 40°N 70°E |
| MO/PA/044 | Desert | 19 | 40°N 80°E |
| MO/PA/045 | Desert/Asiatic semidesert | 16 | 40°N 90°E |
| MO/PA/046 | Desert/semidesert | 19 | 40°N 100°E |
| MO/PA/047* | Desert/semidesert | 30 | 40°N 110°E |
| MO/PA/048 | Desert | 7 | 30°N 40°E |
| MO/PA/049* | Steppe/semidesert | 24 | 30°N 50°E |
| MO/PA/050 | Arid/high steppe | 27 | 30°N 60°E |
| MO/PA/051* | Semidesert/arid steppe | 28 | 30°N 70°E |

Temperate ecological communities.

| | | | |
|---|---|---|---|
| MO/PA/052 | Tundra/birch forest | 14 | Kevo I (1) |
| MO/PA/053 | Tundra/pine forest | 11 | Kevo II (1) |
| MO/PA/054 | Tundra/heathland | 10 | Kevo III (1) |
| MO/PA/056 | Mixed | 15 | Kevo I+II+III (1) |
| MO/PA/057 | Deciduous woodland | 22 | Oxfordshire (2) |
| MO/PA/058 | Woodland/moorland | 25 | Exmoor (3) |
| MO/PA/059 | Alpine tundra | 24 | Abisko (1) |
| MO/PA/060 | Alpine tundra | 21 | Hardangervidda (1) |

Notes: (1): Wielgolaski (1975); (2): Steele & Welch (1972); (3): Allen (1979). Kevo: 69°N 27°E; Abisko: 68°N 19°E; Hardangervidda: 61°N 7°E

## 2. Tropical Habitats.

Within the tropical region the main influence on habitat types is the seasonality and abundance of water availability. In Africa the density of rainfall is distributed symmetrically around the equator and vegetation types tend to mirror the distribution of rainfall (Andrews & Van Couvering, 1975).
The differences between the intensive root systems of grasses and the extensive system of woody plants suits them to different soil and water conditions. Grasses are much better able to stand dry soils and less humid or more seasonal climates, while woody plants are unable to survive in soils that have little water available during extensive periods of drought. Equatorial lowland forest is found in regions of year-round rainfall and gives way to more seasonal forests, woodland, savannah, bushland, semi-desert and desert as increasing aridity gradually takes effect (Andrews & Van Couvering, 1975).

Walter (1973) gives an example of an area in South West Africa across which there is a gradient of gradually increasing summer rainfall. In the arid region the annual rainall amounts to 100mm. per year and only grasses survive. Once the annual rainfall reaches about 300mm. per year, small woody plants are able to survive the dry season and when rainfall reaches 400mm., large solitary trees can be supported. Grasses are

still the dominant partner in this tree-savannah formation and it is they that determine how much water is left for woody plants during the dry season. Once rainfall attains a level where sufficient trees are supported that their crowns link to form a more or less continuous canopy, the resulting shade prevents the proper development of grasses and trees then become dominant. As rainfall increases still further and seasonality decreases, woodland gives way to seasonal forest and finally to tropical evergreen forest in areas where precipitation is abundant throughout the year.

This type of habitat gradient can be almost continuous and since it would be impossible to describe all the intermediate types, only the major habitats are reviewed in this chapter. More complete reviews are given by Money (1965), Eyre (1968), Walter (1973) and Andrews and Van Couvering (1975). Particular reference is made to African habitats since the communities in the modern sample are those used by Andrews et al. (1979), which are all ecological communities from Africa. In the discussion below, these are divided according to described habitat types following the divisions used by Andrews et al., however, it should be noted that when a distance analysis based on ecological structure is used to compare these communities, slightly different groupings result. This receives more discussion on page 225.

a. Tropical Evergreen Forest.

i Habitat and environment.

Forest is defined by Andrews and Van Couvering (1975) as a continuous stand of trees, either evergreen or deciduous, whose crowns intermingle. Abundant year-round rainfall is required for the development of tropical evergreen forest (giving rise to the name "rain-forest") and as a lowland formation it flourishes only in the equatorial zones of South and Central America, Africa, South-east Asia, Indonesia and North-east Australia. These areas between them support three formation types known as the American, African and Indo-Malaysian formations (Whittaker, 1970; Eyre, 1968). All three show the same basic chacteristics and occupy moist lowlands and slopes up to an elevation of about 1000 meters. In areas such as these, high temperatures (a monthly mean of 25 - 26°C) with a small annual range, combine with high humidity resulting from abundant rainfall throughout the year, to produce the hot-house conditions necessary for the development of tropical evergreen forest.

This type of forest can be the most productive of all terrestrial habitats (see table 4.2) and is also the most physically complex of all plant communities

(Walter, 1973). The same types of plant-form are found in all three formations and the most conspicuous feature is the large number of species constituting the tree stratum, some of which can reach heights of up to 60 metres (see table 4.1 and Eyre, 1968). Frequently, the uppermost storey is not compact, but consists of solitary giants rising above the upper canopy which is normally continuous at a height of about 40 or 50 metres. Below this there may be middle and lower stories consisting of dense leaf canopies and the penetration of light through these dense layers of foliage is often so poor that there is little undergrowth at ground level. Although about 70% of the species growing in tropical rain forest are trees, there are also many species of climbers and epiphytes, which attain better light conditions by using large trees for support.

The environment of evergreen forest is practically non-seasonal and any periodicity of growth and flowering, if it exists at all, is not bound to a twelve month cycle. There is no season of general leaf fall like that found in temperate deciduous forests and although some trees occasionally lose all their leaves at once, this appears to be rare and there is usually no relationship to any annual climatic regime (Money, 1965).

ii Ecological diversity of mammal communities.

The sample of mammal communities from tropical evergreen forest consists of two communities, one from Zaire and the other from Guinea. Table 4.4 gives the ranges and means of the number of species and proportion of the total communities falling in each ecological diversity class and figure 4.6 illustrates the means in the form of Ecological Diversity distributions. The two communities contain 75 and 76 species (giving a mean species richness of 75.5) and the size of these communities suggests a habitat of high productivity and stability. This is supported by the body weight distribution and particularly by the number of large-bodied species. In spite of this, however, small species dominate these communities and species with a body weight of less than 10Kg. form at least 75% of the community. This suggests that food resources with a relatively high energy yield are readily available and this is confirmed by the abundance of insectivores, herbivore-frugivores, herbivore-insectivores, and by the presence of frugivores. These four dietary classes together account for 50% of the community. The importance of woody vegetation and trees in particular, is shown by the number of browsers and the number of arboreal and scansorial species. A mean of 35% of the species are tree-dwellers and a further 32% are small ground-adapted mammals that can often

climb facultatively. This pattern also points to the fact that an abundance of edible resources are to be found in the various levels of the canopy zone, while the relative paucity of grazers shows that grasses are of minor importance.

Table 4.4 & Figure 4.6.

Ecological diversity of ecological communities from tropical evergreen forest.

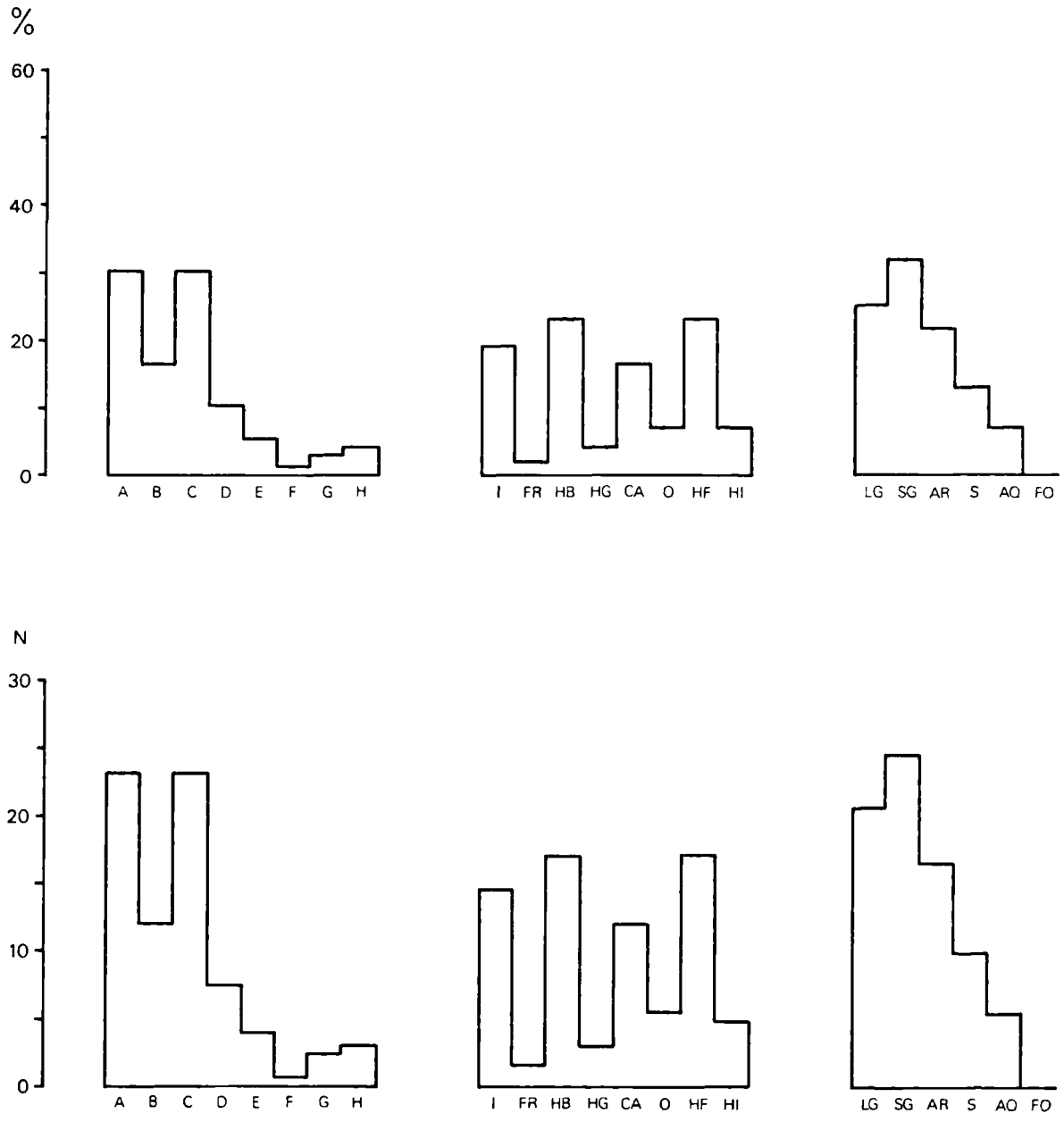
Size range: 75 - 76 species.

Mean size: 75·5 species.

Number of communities: 2.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 30·3 - 30·7 | 30·5 | 23 | 23·0 |
| B | 15·8 - 16·0 | 15·9 | 12 | 12·0 |
| C | 28·9 - 32·0 | 30·4 | 22 - 24 | 23·0 |
| D | 9·3 - 10·5 | 9·9 | 7 - 8 | 7·5 |
| E | 5·3 | 5·3 | 4 | 4·0 |
| F | 0·0 - 1·3 | 0·7 | 0 - 1 | 0·5 |
| G | 2·7 - 3·9 | 3·3 | 2 - 3 | 2·5 |
| H | 3·8 - 4·0 | 3·9 | 3 | 3·0 |
| Diet classes | | | | |
| I | 17·3 - 21·1 | 19·2 | 13 - 16 | 14·5 |
| FR | 1·3 - 2·6 | 1·9 | 1 - 2 | 1·5 |
| HB | 22·4 - 22·7 | 22·5 | 17 | 17·0 |
| HG | 2·6 - 5·3 | 3·9 | 2 - 4 | 3·0 |
| CA | 15·8 - 16·0 | 15·9 | 12 | 12·0 |
| O | 6·6 - 8·0 | 7·3 | 5 - 6 | 5·5 |
| HF | 22·4 - 22·8 | 22·6 | 17 | 17·0 |
| HI | 6·5 - 6·7 | 6·6 | 5 | 5·0 |
| Locomotor classes | | | | |
| LG | 25·0 - 25·4 | 25·2 | 19 | 19·0 |
| SG | 30·3 - 34·7 | 32·5 | 23 - 26 | 24·5 |
| AR | 21·1 - 22·7 | 21·9 | 16 - 17 | 16·5 |
| S | 12·0 - 14·5 | 13·25 | 9 - 11 | 10·0 |
| AQ | 5·3 - 9·2 | 7·25 | 4 - 7 | 5·5 |
| FO | 0·0 | 0·0 | 0 | 0·0 |

Figure 4.6


%
60
40
20
0
A B C D E F G H
I FR HB HG CA O HF HI
LG SG AR S AQ FO
N
30
20
10
0
A B C D E F G H
I FR HB HG CA O HF HI
LG SG AR S AQ FO

b. Tropical Montane Forest.

i Habitat and environment.

Formations similar to lowland evergreen forest are also found in areas of higher elevation. Tropical montane forest occurs where masses of moisture-laden air cause abundant rainfall as they rise to pass over highlands. The base of submontane or intermediate forest usually occurs at about 1000 metres. Montane forest is found under similar conditions at higher elevations and also at cloud level, where humidity reaches a maximum. Montane and cloud forests are usually different in structure from their lowland counterparts and one of the most conspicuous differences is that as temperatures become cooler at higher altitudes, warmth-loving epiphytes are replaced by ferns and lycopods (Walter, 1973). These slightly less favorable growing conditions are also reflected by the fact that the productivity of montane forests is less than that of lowland formations.

ii Ecological diversity of mammal communities.

The montane forest sample consists of 3 communities from Kenya, Uganda and Zaire. Table 4.5 summarizes these communities and the mean values of the number and the proportion of species in each ecological diversity class is plotted in figure 4.7. The species richness of these communities ranges between 55 and 64

species with a mean of 61.0. The overall size of these communities shows that montane forest is less productive than lowland evergreen forest. However, in spite of this the overall patterns of communities from the two habitats are very similar. Montane forest communities differ mainly in that species of less than 100g. body weight (weight class A) form a relatively larger proportion of the total community, although the actual number of species involved is not greater. Within the dietary classes, insectivores, browsing herbivores and carnivores are less numerous than in lowland evergreen forest, but they maintain their relative importance within the community. The most notable difference is that herbivore-frugivores are much less abundant than in lowland formations. The locomotor diversity of communities from the two habitats also shows the same overall appearance although the relative importance of ground-adapted mammals is greater and that of arboreal and scansorial species is less in montane forest communities. The main factor responsible for these differences seems to be the reduced productivity in montane communities, particularly it appears, in the resources available for herbivore-frugivores. Species of this dietary habit are frequently tree-dwellers falling in the range of size classes B and C, which may explain some of the other structural differences between lowland and montane forest communities.

Table 4.5 & Figure 4.7.

Ecological diversity of ecological communities from tropical montane forest.

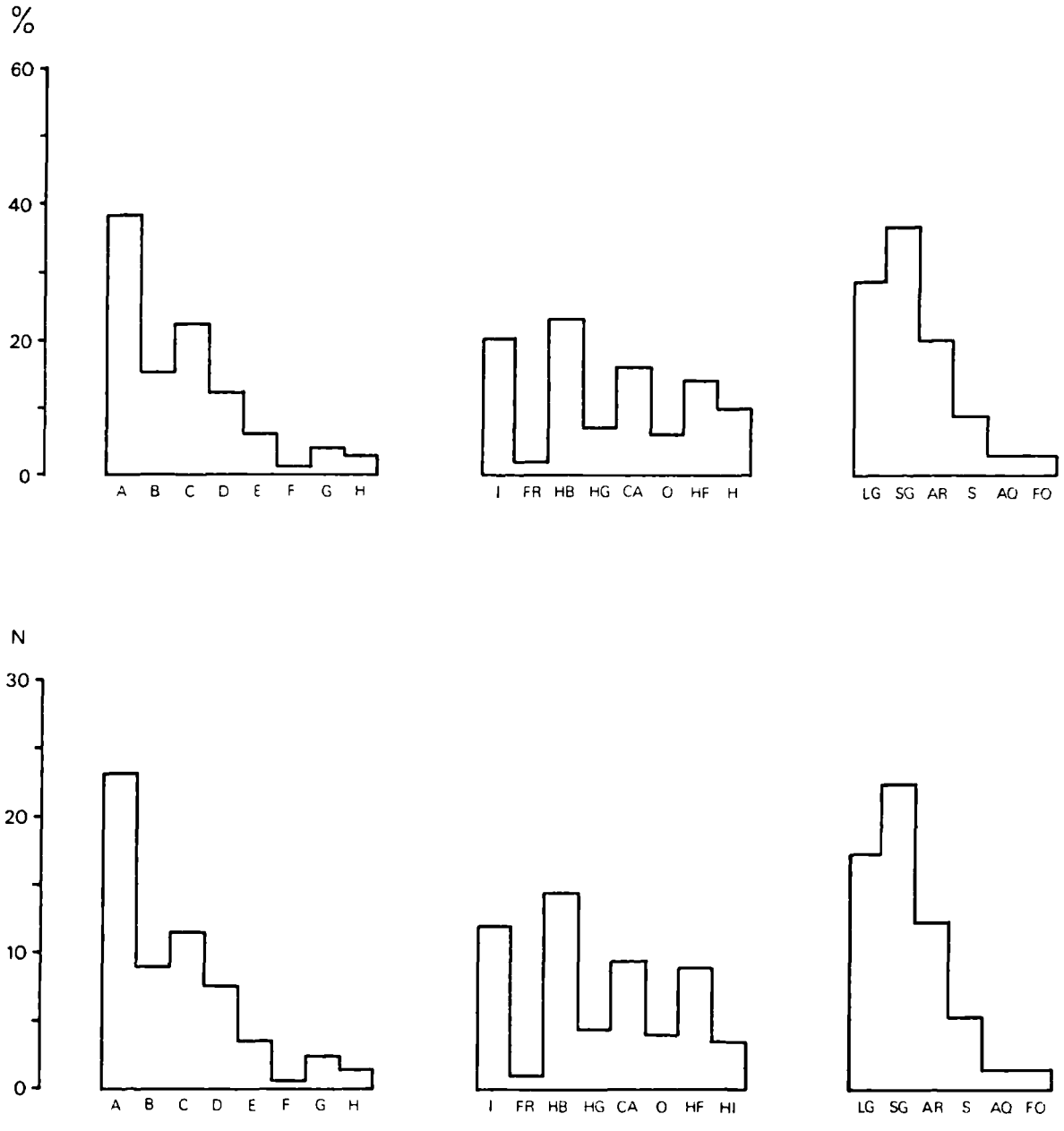
Size range: 55 - 64 species.

Mean size: 61·0 species.

Number of communities: 3.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 34·4 - 40·6 | 37·7 | 21 - 26 | 23·0 |
| B | 14·1 - 15·6 | 14·7 | 8 - 10 | 9·0 |
| C | 20·0 - 23·4 | 21·8 | 11 - 15 | 13·3 |
| D | 9·4 - 15·6 | 12·0 | 6 - 10 | 7·3 |
| E | 3·1 - 9·1 | 6·2 | 2 - 5 | 3·7 |
| F | 0·0 - 1·6 | 0·5 | 0 - 1 | 0·3 |
| G | 3·1 - 5·5 | 4·4 | 2 - 3 | 2·7 |
| H | 1·6 - 4·7 | 2·7 | 1 - 3 | 1·7 |
| Diet classes | | | | |
| I | 15·6 - 23·4 | 19·7 | 10 - 15 | 12·0 |
| FR | 0·0 - 3·1 | 1·6 | 0 - 2 | 1·0 |
| HB | 18·8 - 29·7 | 23·4 | 12 - 19 | 14·3 |
| HG | 7·3 - 7·8 | 7·6 | 4 - 5 | 4·7 |
| CA | 15·6 - 16·4 | 15·9 | 9 - 10 | 9·7 |
| O | 6·3 - 7·4 | 6·7 | 4 | 4·0 |
| HF | 10·9 - 17·2 | 14·6 | 6 - 11 | 9·0 |
| HI | 7·8 - 14·5 | 10·6 | 5 - 8 | 6·3 |
| Locomotor classes | | | | |
| LG | 23·4 - 35·9 | 28·8 | 15 - 23 | 17·7 |
| SG | 34·4 - 37·1 | 36·6 | 20 - 25 | 22·3 |
| AR | 18·8 - 21·9 | 20·2 | 11 - 14 | 12·3 |
| S | 6·3 - 10·9 | 8·9 | 4 - 6 | 5·3 |
| AQ | 1·6 - 3·6 | 2·8 | 1 - 2 | 1·7 |
| FO | 1·8 - 3·1 | 2·7 | 1 - 2 | 1·7 |

Figure 4.7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c. Tropical Seasonal Forests.

i. Habitat and environment.

Regional variations in climate affect the nature of tropical forests and the most important factor is the occurrence of dry periods or prevailing dry winds. Evergreen forest usually gives way to one of three formation types: Montane forest with increasing altitude, simpler evergreen forest towards wet but cooler climates and seasonal forest towards drier or more seasonal climates.

Tropical rainforest relies on copious and reliable rainfall throughout the year, tropical seasonal forests occur in humid tropical areas that have a pronounced dry season. Wherever rainfall becomes light or unreliable, even for a short season, tropical evergreen rain forest gives way to some kind of seasonal forest formation that is better adapted to periodic water deficiency. This usually involves some degree of deciduousness and as the climate becomes drier, deciduous trees becomes more common and at the same time canopy height and coverage both tend to decrease (Whittaker, 1970). Vegetation can vary from luxuriant forest in areas with only a short dry season, through drier deciduous forests to open woodland (Money, 1965; Eyre, 1968; Whittaker, 1970; Walter, 1973). Even when a short dry season occurs, the periodicity of growth and

flowering of tree species adapts itself to the annual cycle with the result that productivity is normally less than that of evergreen forests (see table 4.2).

The most luxuriant type of seasonal forest is known as semi-evergreen forest. It consists of a mixture of evergreen and deciduous species and can sometimes include evergreen species that are facultatively deciduous. Epiphytes are much rarer than in rain forest and there is a tendency towards a two layered structure with an evergreen lower canopy and a deciduous upper storey. Semi-evergreen seasonal forests are found in a three layered form in Africa where the upper layer is deciduous and the lower two evergreen (Eyre, 1968). Where the dry season is more protracted, a formation known as deciduous seasonal forest develops. This is characterised by a discontinuous upper storey and a lower canopy which is more continuous but contains only a proportion of evergreen species. Lianes occur in low numbers and epiphytes are almost totally absent. With a further decrease in rainfall all tree species become deciduous and a deciduous forest or woodland formation results. According to Eyre (1968) the deciduous forest formation is not found in its typical form in Africa and the equivalent seems to be deciduous woodland.

ii Ecological Diversity of mammal communities.

The sample from tropical seasonal forests consists of 6 communities from Tanzania, Kenya and Uganda. The ecological diversity of these communities is summarized in table 4.6 with mean values plotted in figure 4.8. Species richness varies between 57 and 73 with a mean value of 63.3 species. In spite of the fact that the mean species richness of these communities is less than that of lowland evergreen forest communities, the overall pattern of ecological diversity is strikingly similar. The lower species richness suggests that the productivity of seasonal forests is, on average, less than that of evergreen forests. The most marked difference between the two types of community is in the distribution of locomotor adaptations: Ground adapted mammals are much more important, while arboreal and scansorial species are much less important in seasonal than in evergreen forests. Although on the face of it this may suggest that the physical structure of seasonal forests is less complex, it is also likely that the reduced importance of tree-living species is linked with deciduousness of the tree canopy. One natural consequence of seasonality is that productivity varies from season to season. In tropical seasonal forests the most significant effects of seasonal variations seem to take place in the canopy, and the abundance of arboreal specialists is limited by the productivity of this zone during the least favorable part of the year. The number

and relative importance of browsing herbivores and herbivore-frugivores is correspondingly reduced, while omnivores and grazers become more common than in evergreen forest. The availability of high energy yielding food sources is frequently seasonal and the increased importance of low energy food is not only demonstrated in the distribution of dietary specializations, but might also explain the minor differences between the body weight distributions for seasonal and evergreen forests.

Table 4.6 & Figure 4.8.

Ecological diversity of ecological communities from tropical seasonal forest.

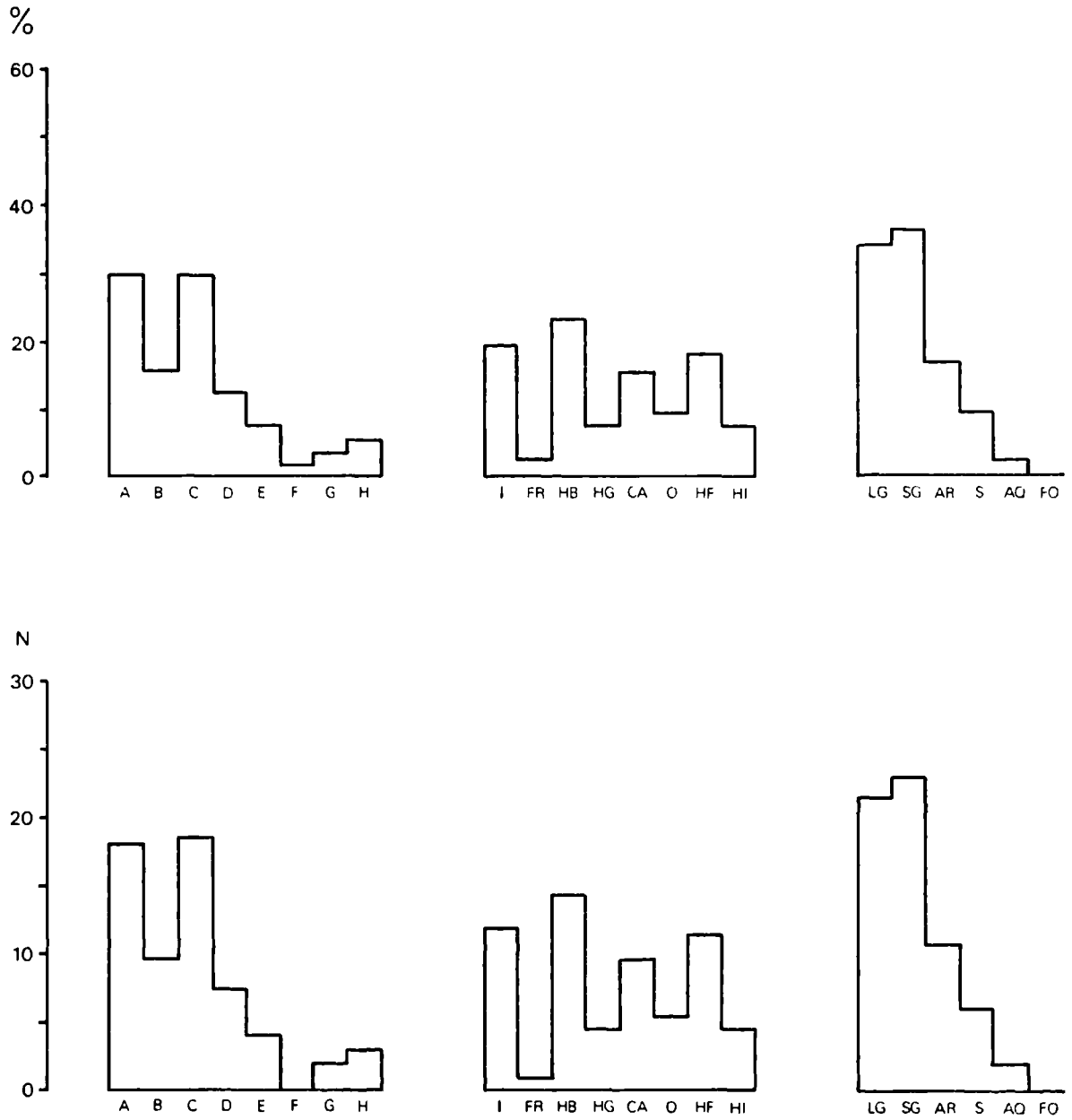
Size range: 57 - 73 species.

Mean size: 63·3 species.

Number of communities: 6.

| | % range | %mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 22·6 - 35·1 | 28·6 | 14 - 22 | 18·2 |
| B | 11·5 - 20·1 | 15·0 | 7 - 12 | 9·5 |
| C | 26·3 - 31·5 | 28·9 | 15 - 23 | 18·3 |
| D | 9·6 - 17·7 | 12·1 | 6 - 11 | 7·6 |
| E | 5·0 - 7·5 | 6·6 | 3 - 5 | 4·2 |
| F | 0·0 - 1·6 | 0·5 | 0 - 1 | 0·2 |
| G | 1·6 - 5·5 | 3·1 | 1 - 4 | 2·0 |
| H | 2·7 - 8·3 | 5·4 | 2 - 5 | 3·3 |
| Diet classes | | | | |
| I | 14·8 - 22·8 | 18·9 | 9 - 15 | 12·0 |
| FR | 0·0 - 3·5 | 1·6 | 0 - 2 | 1·0 |
| HB | 20·9 - 27·9 | 23·2 | 12 - 17 | 14·7 |
| HG | 4·1 - 11·3 | 7·2 | 3 - 7 | 4·5 |
| CA | 12·3 - 17·7 | 15·3 | 8 - 11 | 9·7 |
| O | 7·0 - 12·3 | 8·8 | 4 - 8 | 5·5 |
| HF | 12·9 - 21·9 | 17·75 | 8 - 16 | 11·3 |
| HI | 4·8 - 10·4 | 7·2 | 3 - 7 | 4·7 |
| Locomotor classes | | | | |
| LG | 24·7 - 41·9 | 34·3 | 18 - 26 | 21·5 |
| SG | 32·9 - 38·3 | 36·1 | 20 - 25 | 22·8 |
| AR | 11·3 - 23·3 | 17·4 | 7 - 17 | 11·2 |
| S | 6·5 - 13·7 | 9·0 | 4 - 11 | 5·8 |
| AQ | 0·0 - 5·5 | 2·3 | 2 - 4 | 1·9 |
| FO | 0·0 - 1·6 | 0·3 | 0 - 1 | 0·2 |

Figure 4.8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d. Tropical Woodland.

i Habitat and environment.

Andrews and van Couvering (1975) described woodland as a formation where trees form a more or less closed canopy and Ovington (1972) reinforces the opinion that woodland consists of a continous but fairly light tree cover. The trees are mostly deciduous and adapted to surviving dry conditions. The dominant trees are usually no more than 20 metres high and are mainly flat topped and spreading, forming a canopy which is normally single layered, although there is often no obvious stratification (Andrews and van Couvering, 1975). Bushes and shrubs occur sporadically and grasses and herbs are also consistently present (Andrews and van Couvering, 1975; Ovington, 1972; van Couvering, 1980; Eyre, 1968). Woodland is the most seasonal of the tree dominated habitats and it occurs in areas where there is usually a prolonged seasonal drought of 4 to 7 months (Eyre, 1968). In these environments trees flower, fruit and leaf seasonally and do not provide a constant food supply. Productivity is consequently less than that of forest formations and is concentrated during the growing season when water is most readily available.
As seasonality increases further, true woodland gives way to a savannah-woodland ecotone and thence to the grass-dominated habitats of the savannah.

ii Ecological diversity of mammal communities.

The tropical woodland sample consists of 3 communities from Tanzania ranging in size between 48 and 74 species with a mean species richness of 59.6. Table 4.7 gives a summary of the ecological diversity of these communities. The mean values for each adaptational class are plotted in figure 4.9. Mammal communities from tropical woodland have an adaptational structure that is quite different from that of forest communities. The species richness shows that the productivity of the habitat can be similar to that of seasonal forests, but the number and relative importance of large-bodied species indicates a habitat where low energy yielding resources are most important. The latter point is substantiated by the comparative rarity of insectivores, frugivores, herbivore-frugivores and herbivore-insectivores and the dominance of browsing and grazing herbivores. In line with this, the locomotor distribution is dominated by ground adapted mammals, while arboreal and scansorial species are rare. This suggests a lack of physical complexity and a comparative poverty of edible resources in the trunk, branch and canopy zones of the habitat.

Table 4.7 & Figure 4.9.

Ecological diversity of ecological communities from tropical woodland.

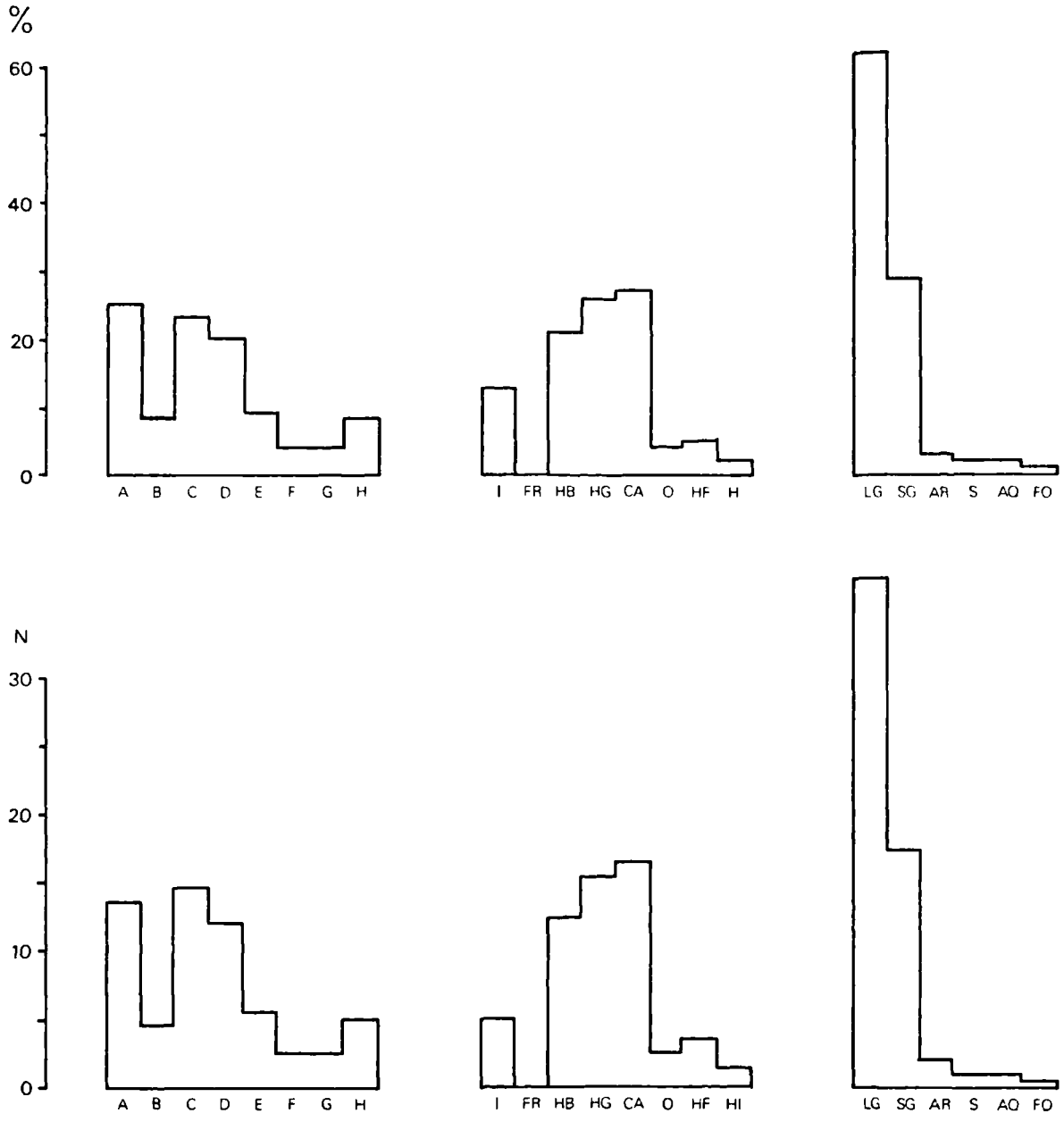
Size range: 48 - 74 species.

Mean size: 59·7 species.

Number of communities: 3.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 19·3 - 27·1 | 24·7 | 11 - 16 | 13·3 |
| B | 5·4 - 10·4 | 7·6 | 4 - 5 | 4·3 |
| C | 14·6 - 29·8 | 23·4 | 7 - 19 | 14·3 |
| D | 17·5 - 21·6 | 20·0 | 10 - 16 | 12·0 |
| E | 7·0 - 10·4 | 9·0 | 4 - 7 | 5·3 |
| F | 4·1 - 5·3 | 4·5 | 2 - 3 | 2·7 |
| G | 4·1 - 5·3 | 4·5 | 2 - 3 | 2·7 |
| H | 8·1 - 8·8 | 8·4 | 4 - 6 | 5·0 |
| Diet classes | | | | |
| I | 10·5 - 16·7 | 13·1 | 6 - 9 | 5·0 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 20·3 - 21·1 | 20·7 | 10 - 15 | 12·3 |
| HG | 22·8 - 31·3 | 26·3 | 13 - 18 | 15·3 |
| CA | 20·8 - 33·3 | 27·0 | 10 - 20 | 16·3 |
| O | 2·1 - 6·8 | 4·1 | 1 - 5 | 2·6 |
| HF | 5·3 - 8·3 | 5·3 | 3 - 4 | 3·3 |
| HI | 0·0 - 4·1 | 2·5 | 0 - 3 | 1·7 |
| Locomotor classes | | | | |
| LG | 56·3 - 66·2 | 62·5 | 27 - 49 | 37·7 |
| SG | 27·0 - 33·3 | 29·5 | 16 - 20 | 17·3 |
| AR | 2·7 - 4·2 | 3·5 | 2 | 2·0 |
| S | 1·4 - 2·1 | 1·8 | 1 | 1·0 |
| AQ | 1·4 - 2·1 | 1·8 | 1 | 1·0 |
| FO | 0·0 - 2·1 | 1·2 | 0 - 1 | 0·7 |

Figure 4.9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e. Tropical Bushland.

i Habitat and environment.

Tropical bushland is a formation where grass is found in conjunction with a dominant cover of low, bushy, deciduous trees and shrubs which are normally less than 6 metres tall (Andrews & van Couvering, 1975; van Couvering, 1980; Eyre, 1968). Large trees may also be present. This type of habitat is found in the Americas, Asia, Australasia and Africa in areas of low rainfall where there is sufficient moisture during most of the year to support low woody vegetation with deep extensive root systems but insufficient to support extensive stands of larger trees associated with woodland formations (Money, 1965). At present, bushland appears to be increasing at the expense of savannah and woodland, mainly as the result of shifting agriculture and overgrazing (Andrews & Van Couvering, 1975). The physical structure and productivity of bushland appears in most respects to be similar to that of woodland.

ii Ecological diversity of mammal communities.

Bushland habitats are represented by a sample of 4 communities from Kenya and Uganda. The ranges and means of the Ecological Diversity distributions of these communities are given in table 4.8 and the means plotted as Ecological Diversity histograms in figure 4.10.

Species richness of the four communities ranges from 54 to 72 with a mean of 63.75 species. The size of these communities suggests that the productivity of this habitat is similar to that of woodland and taken as a whole, the ecological diversity of bushland communities is very similar to those from woodland habitats. Large-bodied species are of similar importance in both, insectivores, browsers and omnivores are more numerous and grazers less numerous than in woodland, although low-energy resources are still the most important. The pattern of locomotor adaptations is very similar to that of woodland communities, being dominated by ground adapted forms and particularly by large ground adapted species. Other locomotor types are present, but only in small numbers. The overall impression given by these communities is that they originate in habitats that are very similar to tropical woodland in productivity, stability, and structural complexity.

Table 4.8 & Figure 4.10.

Ecological diversity of ecological communities from tropical bushland.

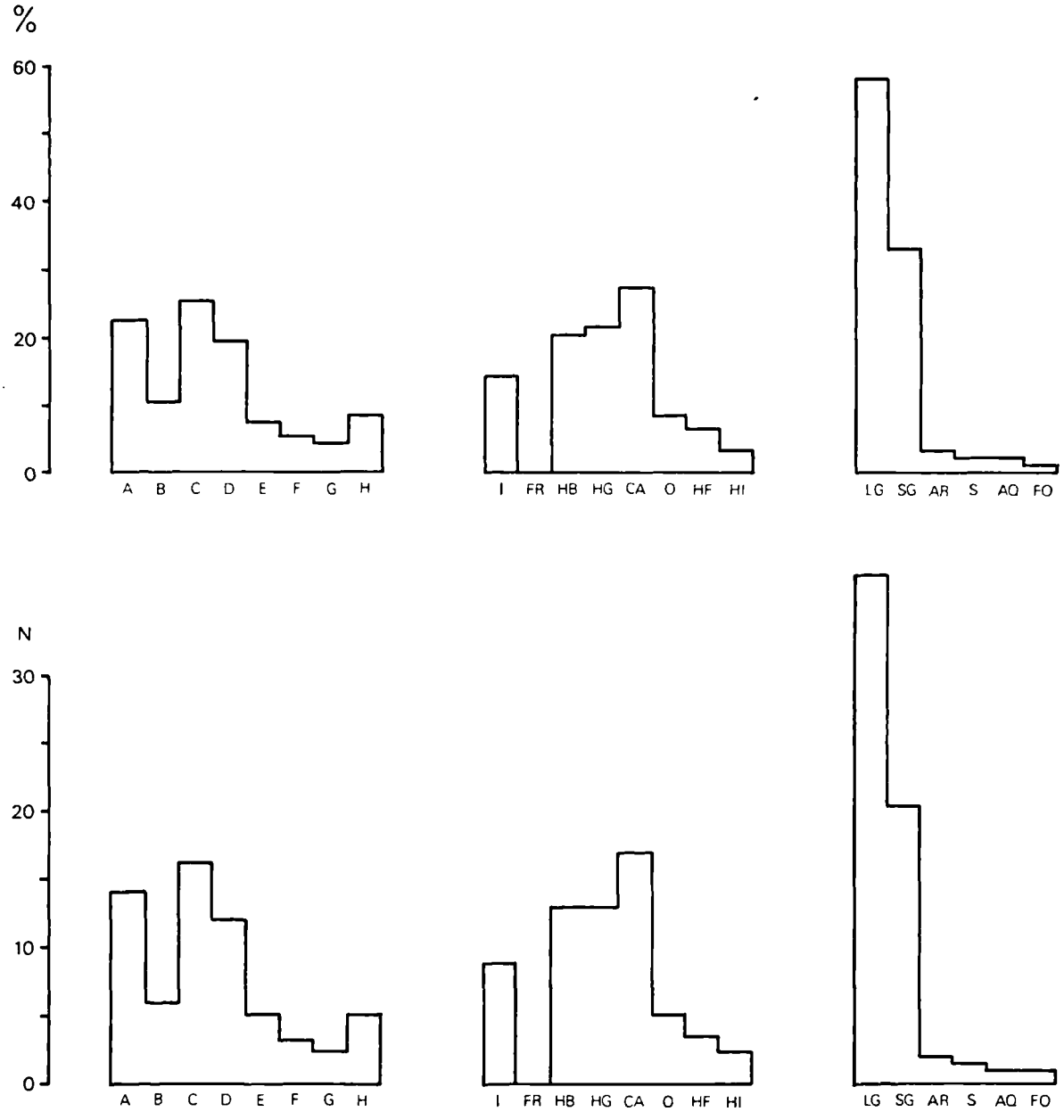
Size range: 54 - 72 species.

Mean size: 63·75 species.

Number of communities: 4.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 17·5 - 25·9 | 22·4 | 11 - 18 | 14·2 |
| B | 8·3 - 12·7 | 9·8 | 5 - 8 | 6·2 |
| C | 22·7 - 27·7 | 24·9 | 15 - 17 | 15·7 |
| D | 14·8 - 22·7 | 18·7 | 8 - 15 | 12·0 |
| E | 6·1 - 9·7 | 7·4 | 4 - 7 | 4·7 |
| F | 3·7 - 6·1 | 5·1 | 2 - 4 | 3·2 |
| G | 3·0 - 4·8 | 3·9 | 2 - 3 | 2·5 |
| H | 6·9 - 9·1 | 7·8 | 4 - 6 | 5·0 |
| Diet classes | | | | |
| I | 11·1 - 20·4 | 14·4 | 7 - 11 | 9·0 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 13·0 - 27·3 | 20·0 | 7 - 18 | 13·0 |
| HG | 19·4 - 22·2 | 20·8 | 12 - 14 | 13·2 |
| CA | 24·2 - 30·2 | 26·7 | 14 - 19 | 17·0 |
| O | 6·1 - 9·7 | 7·8 | 4 - 7 | 5·0 |
| HF | 3·0 - 9·3 | 6·1 | 2 - 5 | 3·7 |
| HI | 1·9 - 8·3 | 3·4 | 1 - 6 | 2·7 |
| Locomotor classes | | | | |
| LG | 57·9 - 63·6 | 58·5 | 28 - 43 | 37·5 |
| SG | 28·8 - 37·0 | 32·7 | 19 - 23 | 20·7 |
| AR | 1·6 - 4·2 | 3·2 | 1 - 3 | 2·0 |
| S | 1·5 - 3·7 | 2·4 | 1 2 | 1·5 |
| AQ | 0·0 - 3·7 | 2·1 | 0 - 2 | 1·2 |
| FO | 1·4 - 1·6 | 1·1 | 0 1 | 0·7 |

Figure 4.10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I FR HB HG CA O HF HI
LG SG AR S AQ FO

f. Savannah and Tropical Grassland.

i Habitat and environment.

Savannah is a collective term for a range of physiognomically similar plant communities in which grasses are predominant (Eyre, 1968; Janis, 1982). It is defined by Walter (1973) as an homogenous tropical grassland which has a more or less even scattering of trees. The amount of tree cover can vary enormously, but when woody plants are entirely lacking the habitat is usually referred to as tropical grassland. A detailed description of different types of savannah and grassland can be found in Eyre (1968).

The transition from woodland through savannah-woodland to open savannah is a gradual one and in Africa it is difficult to draw a clear dividing line between open woodland and savannah. Even in woodland, woody plants are rarely so dense that grasses are entirely precluded (Eyre, 1968). Savannah is similar to woodland except that in savannah the trees tend to be more widely spaced (Andrews & Van Couvering, 1975). Savannah occurs in areas that are too dry for the development of forest formations either because of the nature of the soil (edaphic savannah) or because of the climate (climatic savannah) (Whittaker, 1970). Walter (1973) recognised the existence of a "savannah climate" where annual rainfall is between

500mm. and 100 or 200mm. a year. Drier conditions lead to the development of desert shrub or desert conditions (Andrews and van Couvering, 1975). However, grasslands can seemingly be formed in all vegetational habitats as a result of edaphic factors or other influences. According to Andrews and van Couvering (1976), they do not form part of the latitudinally zoned sequence in Africa and are mainly edaphic in origin although some areas of non-edaphic grassland are apparently the result of fire.

Money (1965) also believed that there is no savannah climate as such, but did recognise a strong relationship with moisture content of the general environment and soils in particular. Grasses tend to occur in less well watered areas particularly where there is some seasonal deficiency of water, but if the surface dries completely while there is still water at depth, where it can be reached by the extensive root systems of woody plants, grasses do not compete well with shrubs and trees. The balance between grasses and woody vegetation thus depends on the relationship between moisture in the surface layers of the soil profile and that found deeper in the ground, but the nature of the competition between the two types of plant is such that whichever predominates, it tends to produce conditions that ensure its own survival (Money, 1965; Eyre, 1968). The important difference lies in the root

systems and water economy. Grasses have shallow but intensive root systems, transpire strongly, show a large production in a short time, and die back during periods of drought. In this way they cease transpiration in dry seasons once the above-ground growth has died off and they are able to survive long periods of drought. Woody plants have deep and extensive root systems and transpire year-round. If there is no water available during the dry season then woody vegetation is unable to survive (Walter, 1973). In many areas this equilibrium is easily disrupted by factors such as fire and grazing pressure which can tip the balance in favour of grassland, although over grazing of grassland can act in the favour of woody plants (Walter, 1973).

The productivity of savannah is usually less than that of forest formations in the tropical latitides although high levels of productivity can be attained (see table 4.2). Savannahs and tropical grassland contain very few woody species and structural complexity is generally low.

ii Ecological diversity of mammal communities.

The grassland and savannah sample is represented by one community from the short grass plains of Serengeti in Tanzania and 3 flood plain communities from Zambia, Tanzania and Kenya. These have been analysed

separately since communities from the two habitats seem to show slightly different patterns of ecological diversity.

The short grass plains community contains 41 species, which suggests that the productivity of this habitat is low in relation to that of habitats dominated by woody plants. The weight distribution is similar to those of woodland and bushland communities. The importance of low energy foodstuffs is shown by the paucity of frugivores, omnivores, herbivore-frugivores and herbivore-insectivores. Browsing and grazing herbivores together make up one-third of the community and the importance of grass as a foodsource is reflected in the fact that grazers outnumber browsers by nearly three to one. The poverty of browse and woody plants in the grassland habitat is also demonstrated by the distribution of locomotor adapatations: With the exception of one scansorial species, all others are ground adapted forms, nearly two-thirds of the community being large ground adapted mammals. The overall ecological diversity of this community thus suggests a habitat of only moderate productivity, where structural complexity is low and grass is the dominant plant resource.

The species richness of the three floodplain communities ranges from 48 to 52 with a mean value of

50.3 species. The size of these communities suggests a relatively low productivity. The ecological diversity of floodplain communities appears to be the same as that of woodland and bushland communities in most respects. In contrast to short grass plains, the existence of woody vegetation is suggested by the presence of arboreal and scansorial species and the fact that browsers as well as grazers form a significant part of the community.

Table 4.9 & Figure 4.11.

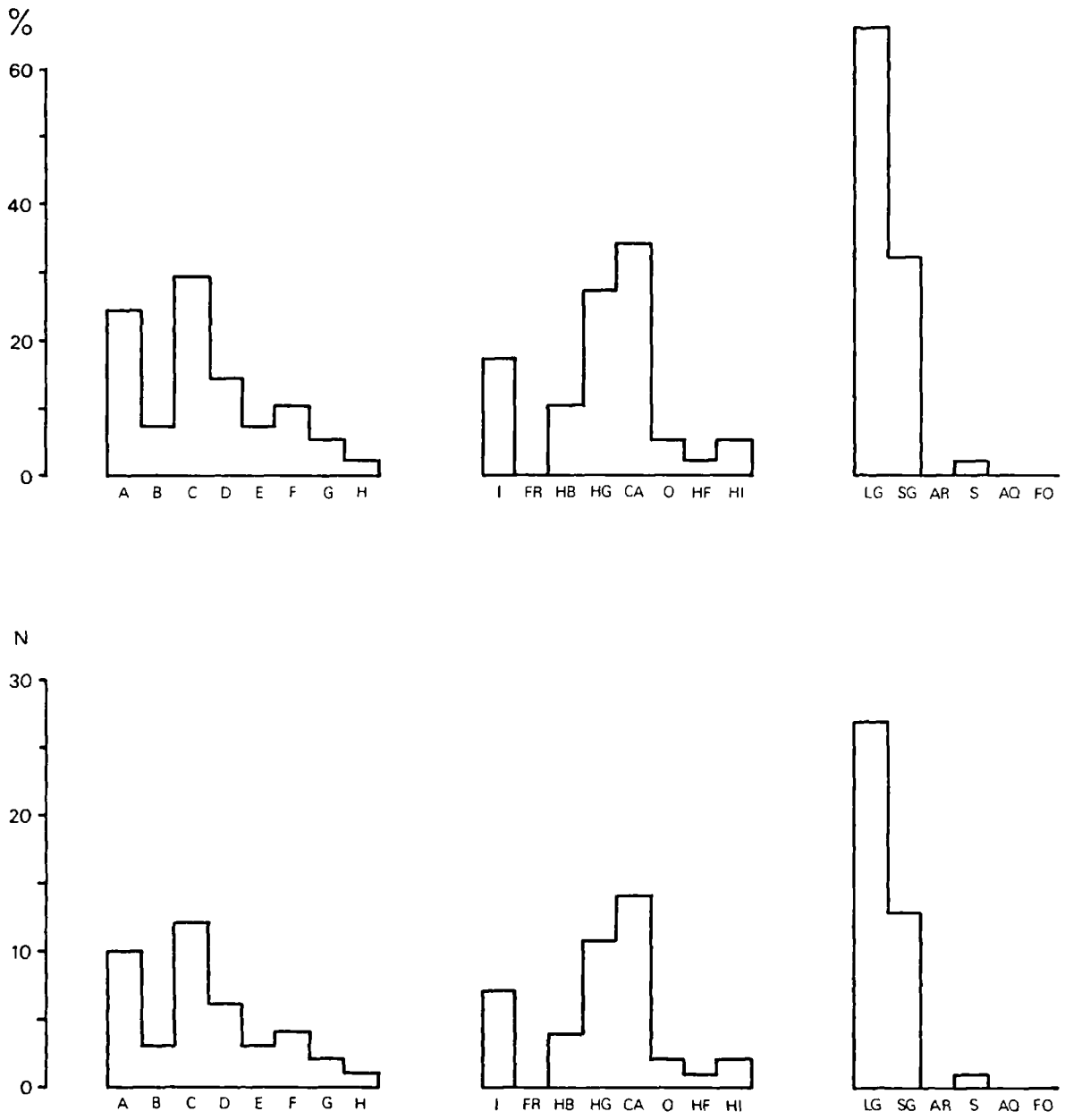
Ecological diversity of ecological communities from tropical short grass plains.

Community size: 41 species.

Number of communities: 1.

| | % | N |
|---|---|---|
| **Weight classes** | | |
| A | 24·4 | 10 |
| B | 7·3 | 3 |
| C | 29·3 | 12 |
| D | 14·6 | 6 |
| E | 7·3 | 3 |
| F | 9·8 | 4 |
| G | 4·9 | 2 |
| H | 2·4 | 1 |
| **Diet classes** | | |
| I | 17·1 | 7 |
| FR | 0·0 | 0 |
| HB | 9·8 | 4 |
| HG | 26·8 | 11 |
| CA | 34·1 | 14 |
| O | 4·9 | 2 |
| HF | 2·4 | 1 |
| HI | 4·9 | 2 |
| **Locomotor classes** | | |
| LG | 65·9 | 27 |
| SG | 31·7 | 13 |
| AR | 0·0 | 0 |
| S | 2·4 | 1 |
| AQ | 0·0 | 0 |
| FO | 0·0 | 0 |

Figure 4.11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I FR HB HG CA O HF HI
LG SG AR S AQ FO

Table 4.10 & Figure 4.12.

Ecological diversity of ecological communities from tropical flood plain habitats.

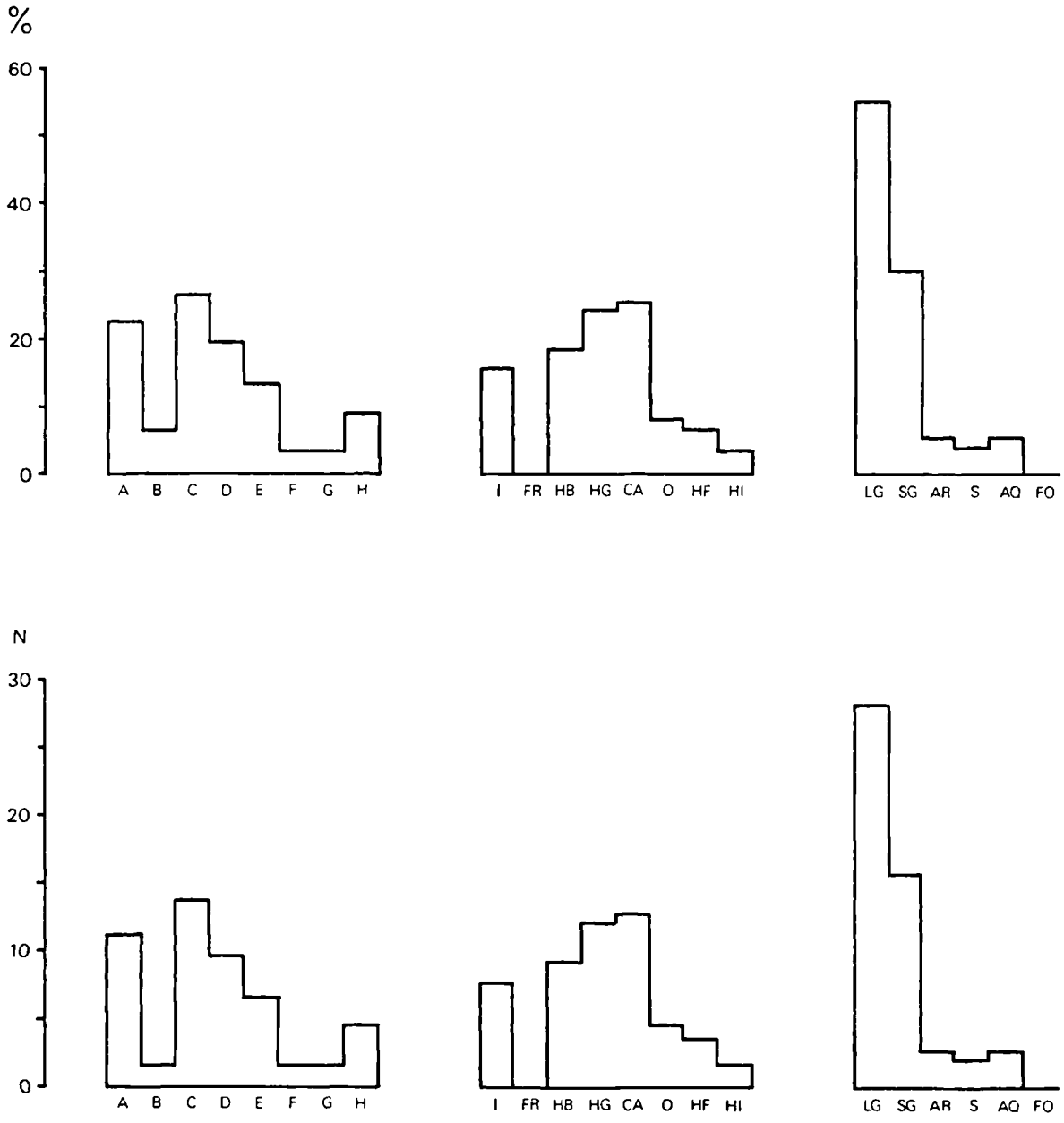
Size range: 48 - 52 species.

Mean size: 50·3 species.

Number of communities: 3.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 18·8 - 23·5 | 21·8 | 9 - 12 | 11·0 |
| B | 2·1 - 7·8 | 5·9 | 1 - 4 | 3·0 |
| C | 19·6 - 36·5 | 26·3 | 10 - 19 | 13·3 |
| D | 15·4 - 22·9 | 19·3 | 8 - 11 | 9·3 |
| E | 5·8 - 16·7 | 12·7 | 3 - 8 | 6·3 |
| F | 1·9 - 4·2 | 3·3 | 1 - 2 | 1·7 |
| G | 1·9 - 4·2 | 2·7 | 1 - 2 | 1·3 |
| H | 7·7 - 9·8 | 8·6 | 4 - 5 | 4·3 |
| Diet classes | | | | |
| I | 12·5 - 17·3 | 15·2 | 6 - 9 | 7·7 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 13·7 - 23·1 | 17·8 | 7 - 12 | 9·0 |
| HG | 15·4 - 29·2 | 24·0 | 8 - 14 | 12·0 |
| CA | 21·2 - 29·2 | 25·3 | 11 - 14 | 12·7 |
| O | 6·3 - 9·8 | 8·6 | 3 - 5 | 4·3 |
| HF | 3·9 - 11·5 | 6·5 | 2 - 6 | 3·3 |
| HI | 1·9 - 3·9 | 2·6 | 1 - 2 | 1·3 |
| Locomotor classes | | | | |
| LG | 46·2 - 64·6 | 55·9 | 24 - 31 | 28·0 |
| SG | 28·8 - 33·3 | 30·4 | 14 - 17 | 15·3 |
| AR | 2·0 - 13·5 | 5·2 | 1 - 7 | 2·7 |
| S | 3·9 - 7·7 | 3·9 | 2 - 4 | 2·0 |
| AQ | 3·8 - 6·3 | 4·7 | 2 - 3 | 2·3 |
| FO | 0·0 | 0·0 | 0 | 0·0 |

Figure 4.12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LG SG AR S AQ FO
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I FR HB HG CA O HF HI
LG SG AR S AQ FO

g. The Modern Tropical Comparative Set.

The modern tropical comparative set consists of 22 of the ecological communities originally used by Andrews et al. (1979). These were described above following the same habitat divisions made by Andrews et al. on the basis of the habitats actually associated with each community. As part of this study, distance matrices were calculated using euclidean distance as described in chapter 3, based either on "N", the number of species in each ecological diversity class, or "%", the proportion of the community in each class. Figure 4.13 shows dendrograms that were drawn up from these matrices using Single Linkage Analysis (Pielou, 1966). Table 4.14 summarizes details of the described habitat, the groups used by Andrews et al. (1979) and the grouping obtained according to the two single linkage dendrograms. Each locality is numbered corresponding to table 1 of Andrews et al. (1979) and the numbered communities with prefixes MO/AF in table 4.3. The grouping given by the single linkage dendrograms is the basis of the groups used in the Residual Diversity analyses of tropical communities and fossil faunas presented later.

As well as being the foundation for the groups used later for Residual Diversity analyses, the dendrograms also illustrate some important points about

the comparative communities themselves. The most apparent division is that between forest and non-forest communities; forest communities are always differentiated from non-forest communities, but communities from the different forest habitats do not always form clear sub-groups. Within the non-forest communities, grassland and woodland-bushland communities share a similar pattern of ecological diversity and cannot be distinguished by proportions. They do, however, differ in size and form separate subgroups in the dendrogram based on absolute numbers. Put into more abstract terms, there is a dichotomy between highly productive, physically complex habitats where high energy food sources are important (Forest types I and II) and habitats of moderate to low productivity, where physical complexity and productivity of the canopy zone are low and where grasses form a significant part of the resource base which is in any case dominated by low energy yielding resources.

Table 4.11 Habitat types of communities in the modern tropical comparative set.

| Community number | Described habitat | Andrews et al. group | Distance matrix group |
|---|---|---|---|
| 1 | Lowland evergreen forest; primary and secondary-riverine cultivation types. | Lowland evergreen forest. | Forest type I. |
| 2 | Floodplain grassland with bordering woodland, many shallow lakes, raised levees. | Floodplain. | Grassland. |
| 3 | Montane evergreen forest, primary and secondary with glades. | Montane forest. | Forest type II. |
| 4 | Lake in short grass plains with fringing woodland. | Woodland. | Woodland-bushland. |
| 5 | Short grass plains, small patches of bush, rocky valleys. | Grassland. | Grassland. |
| 6 | Deciduous woodland and bushland with rocky hillsides. | Woodland. | Woodland-bushland. |
| 7 | Intermediate semi-deciduous forest. | Seasonal forest. | Forest type II. |
| 8 | Floodplain grassland with bordering woodland and lake swamps. | Floodplain. | Grassland. |
| 9 | Intermediate semi-deciduous forest, mainly secondary, with glades and bush-covered hills. | Seasonal forest. | Forest type II. |
| 10 | Floodplain grassland with patches of deciduous forest and shallow lakes. | Floodplain. | Grassland. |
| 11 | Arid bushland with rocky hills. | Bushland. | Woodland-bushland. |
| 12 | Lowland evergreen forest with much cultivation and plantation. | Lowland evergreen forest. | Forest type I. |
| 13 | Wooded grassland and lake flats. | Woodland. | Grassland. |
| 14 | Grassland-bushland mosaic; fire-induced; and narrow riverine woodland. | Bushland. | Woodland-bushland. |
| 16 | Bushland and arid bush, rocky hills, strip of riverine woodland. | Bushland. | Woodland-bushland. |
| 17 | Lowland deciduous forest and woodland. | Seasonal forest. | Forest type II. |
| 18 | Lowland semi-deciduous forest, mainly secondary and monotypic types. | Seasonal forest. | Forest type I. |
| 19 | Lowland semi-deciduous forest. | Seasonal forest. | Forest type I. |
| 20 | Short grass plains-bush-woodland mosaic. | Bushland. | Grassland. |
| 21 | Lowland semi-deciduous forest. | Seasonal forest. | Forest type I. |
| 22 | Montane evergreen forest continuous with the lowland. | Montane forest. | Forest type I. |
| 23 | Montane evergreen forest in river valley. | Montane forest. | Forest type I. |

Figure 4.13. Single linkage dendrogram grouping of communities in the modern tropical comparative set.

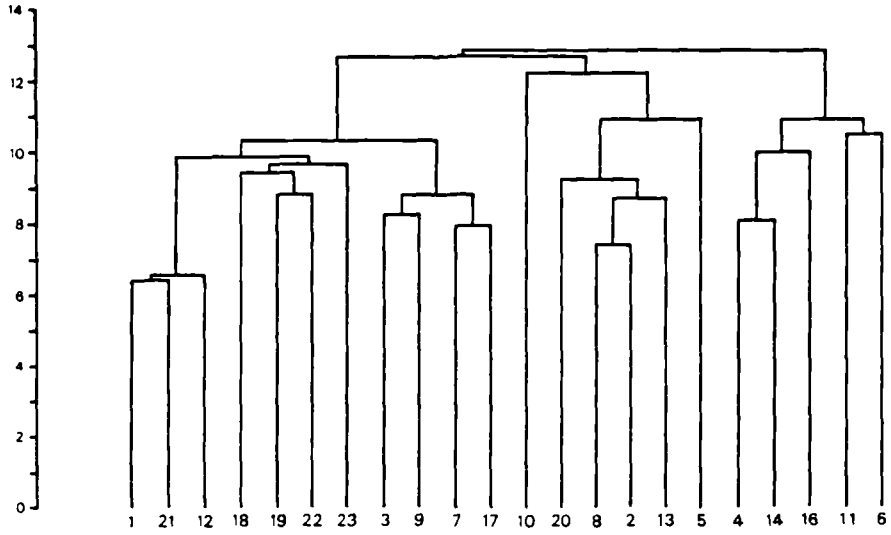
A. Dendrogram based on N, the number of species in each class of the ecological diversity distribution.

B. Dendrogram based on %, the proportion of the community in each class of the ecological diversity distribution.

A summary of the habitat types of the numbered communities figured in these dendrograms is given in table 4.11 (p. 226) and a detailed discussion is to be found in the text (pp. 224-5).

Figure 4.13.

A

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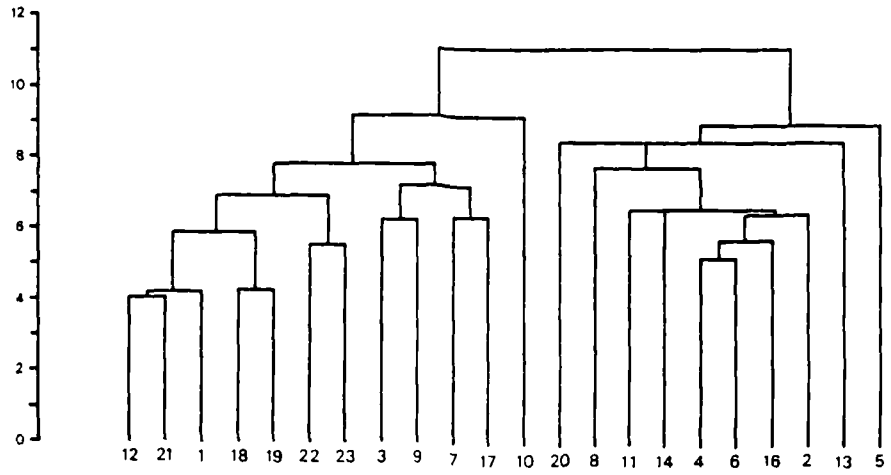


The groups used in Residual Diversity figures based on the modern tropical sample are derived from the dendrograms shown in figure 4.13 and are as follows:

| Community number | Habitat type | Key |
|---|---|---|
| 1, 12, 18, 19, 21, 22, 23. | Forest type I |  |
| 3, 7, 9, 17. | Forest type II |  |
| 4, 6, 11, 14, 16. | Woodland-bushland |  |
| 2, 5, 8, 10, 13, 20. | Savannah-grassland |  |

3. Palaearctic Habitats.

Temperate habitats differ from tropical habitats in that seasonal variations of insolation and temperature are important in addition to rainfall patterns. At the highest latitudes the growing season is so short and the climate so severe that trees are unable to develop. These areas are occupied by treeless tundra which is replaced by coniferous forest where conditions become more hospitable. At lower latitudes where the climate is less severe still and the growing season longer, temperate deciduous forest occurs in humid regions, while steppe replaces deciduous forest as the climate becomes more arid. Areas of extreme aridity support dry steppe, semi-desert and desert. Consequently, when considering temperate habitats, not only do rainfall patterns have to be taken into account, but also seasonality and variations in temperature and day length.

a. Deciduous forest.

1 Habitat and environment.

Deciduous forest communities occupy areas where an abundant annual rainfall of about 30 to 60 inches, distributed more or less evenly throughout the year, is found in conjunction with moderate temperatures which show a marked seasonal pattern. Further south, where moisture remains high but summer-winter temperature differences are less pronounced, deciduous forest gives way to broad-leaved evergreen formations of the mediterranean region. The ecotone with boreal forest, the other major forest formation of temperate latitides, occurs in a mosaic transition zone known as mixed forest. At one time an almost continuous belt of mixed forest extended across Europe, from outliers in Scotland and France, as far as the North European plain (Eyre, 1968). In some places there is also a narrow belt of deciduous forest between the boreal forest and the grassland of the Siberian plain. Another body of temperate deciduous forest is found in eastern China. The fact that the main bulk of the formation occurs at the edges of the continental mass suggests an association with oceanic rather than continental climates.

Deciduous forest regions contrast strongly with those that support boreal forest. A longer, warmer growing season means that the net primary productivity

and standing phytomass of deciduous forests are twice those of the boreal forest (table 4.2 and Walter, 1973). Periodic leaf loss in the temperate region is an adaptation to an annual cold season when low temperatures and frosts block photosynthesis. Deciduous trees must have a growing season of at least 120 days with a mean temperature of more than 10°C, in order to allow them to produce sufficient organic material to survive the periods when they are unable to photosynthesise. This compares with a growing season of 30 days which is all that is necessary for the survival of the coniferous trees of the boreal forest (Walter, 1973).

The European and North American deciduous forest formations are very similar, although the American formation is floristically richer. In the European formation only about a dozen species are common and widespread, whereas in North America, common species number several score (Eyre, 1968; Whittaker, 1970). In both formations there is an upper story of trees which permits a good deal of direct sunlight to penetrate. This allows rich shrub and herb layers to flourish, and the structure of these understory layers is often very complex. However, although a three or four layered community is typical now (consisting of one or two tree canopies, a shrub layer and a herb stratum) it is likely that the true climax is rarely reached and

that natural climax forest probably had a single tree canopy, unlike that of the present day which has suffered considerably at the hands of man (Odum, 1971).

ii Ecological diversity of mammal communities.

The sample of deciduous forest communities consists of 3 geographical communities from western Europe and 2 ecological communities from Britain. Tables 4.12 and 4.13 give the ranges and means of the proportion of the whole community and the number of species in each ecological diversity class. Figures 4.14 and 4.15 illustrate the mean values plotted as Ecological Diversity histograms.

The overall species richness of these communities suggests a habitat of only moderate productivity compared with that of tropical habitats. The weight distribution of deciduous forest communities is dominated by small-bodied species. They contain greater numbers of small bodied species than either tundra, boreal forest or steppe communities and species below 10kg. body weight generally account for all but about 10% of the community. Deciduous forest is the most productive of temperate habitats (see table 4.2) and the notable lack of large-bodied species (which is discussed further in chapter 7) is probably due mainly to the disturbing effect of man on temperate ecosystems.

The dietary distribution is lominated by four classes, insectivores, grazers, carnivores and herbivore-frugivores. This fact, together with the overall size of these communities suggests a habitat with a wide range of resources available. The presence of herbivore-insectivores and omnivores supports this point. Browsers are present, but not in large numbers, which is possibly explained by the fact that trees in this habitat are predominantly deciduous. Browse therefore forms a resource that is only seasonally available and it is consumed largely by herbivore-frugivore species who are also able to exploit foods such as fruit, seeds and bark.

Terrestrial species dominate the locomotor zonation although the consistent presence of arboreal and scansorial species is a strong indication of the importance of trees in the habitat. Apparently neither the continuity of arboreal pathways nor the diversity of resources in tree canopies is sufficient throughout the year to support large numbers of specialist arboreal and climbing species.

Table 4.12 & Figure 4.14.

Ecological diversity of geographical communities from temperate deciduous forest.

Size range: 43 - 51 species.

Mean size: 46·7 species.

Number of communities: 3.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 41·9 - 47·8 | 45·6 | 18 - 24 | 21·4 |
| B | 23·3 - 27·5 | 24·9 | 10 - 14 | 11·7 |
| C | 13·7 - 23·3 | 18·1 | 7 - 10 | 8·3 |
| D | 4·7 - 7·8 | 6·3 | 2 - 4 | 3·0 |
| E | 2·2 - 4·7 | 3·6 | 1 - 2 | 1·7 |
| F | 0·0 - 2·3 | 1·5 | 0 - 1 | 0·7 |
| G | 0·0 | 0·0 | 0 | 0·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 15·2 - 18·6 | 16·5 | 7 - 8 | 7·7 |
| FR | o·o | 0·0 | 0 | 0·0 |
| HB | 5·9 - 9·3 | 8·0 | 3 - 4 | 3·7 |
| HG | 18·6 - 23·9 | 21·4 | 8 - 11 | 10·0 |
| CA | 17·4 - 23·5 | 20·6 | 8 - 12 | 9·7 |
| O | 6·5 - 11·6 | 8·6 | 3 - 5 | 4·0 |
| HF | 16·3 - 21·7 | 19·0 | 7 - 10 | 8·7 |
| HI | 4·7 - 7·8 | 6·3 | 2 - 4 | 3·0 |
| Locomotor classes | | | | |
| LG | 19·6 - 27·9 | 23·1 | 10 - 12 | 10·7 |
| SG | 44·2 - 52·9 | 49·8 | 19 - 27 | 23·3 |
| AR | 9·3 - 13·0 | 10·7 | 4 - 6 | 5·0 |
| S | 3·9 - 4·7 | 4·3 | 0 - 2 | 2·0 |
| AQ | 6·5 - 11·6 | 9·3 | 3 - 5 | 4·3 |
| FO | 2·2 - 3·9 | 2·8 | 1 - 2 | 1·3 |

F gure 4.14

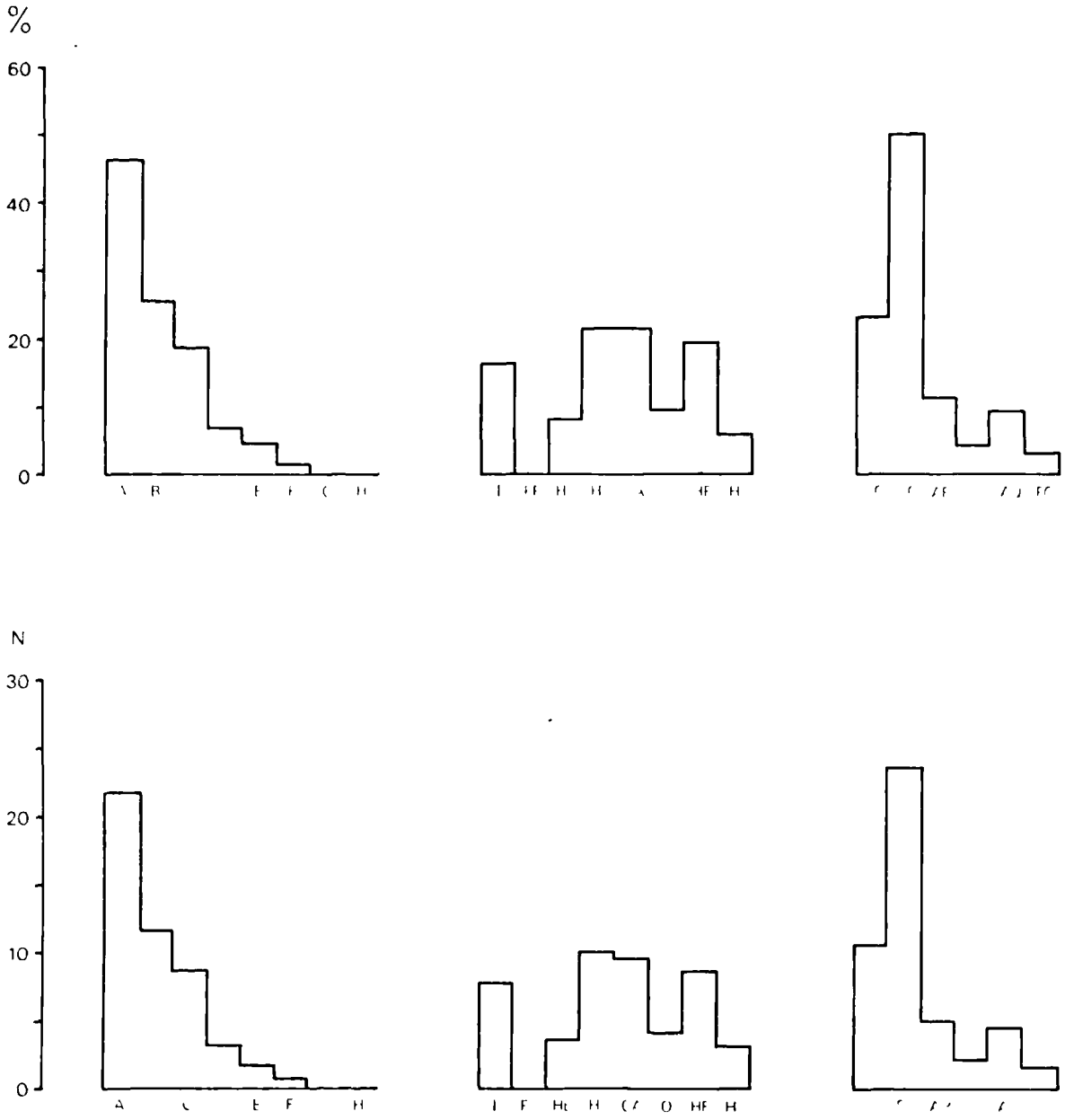


Table 4.13 & Figure 4.15.

Ecological diversity of ecological communities from temperate deciduous forest.

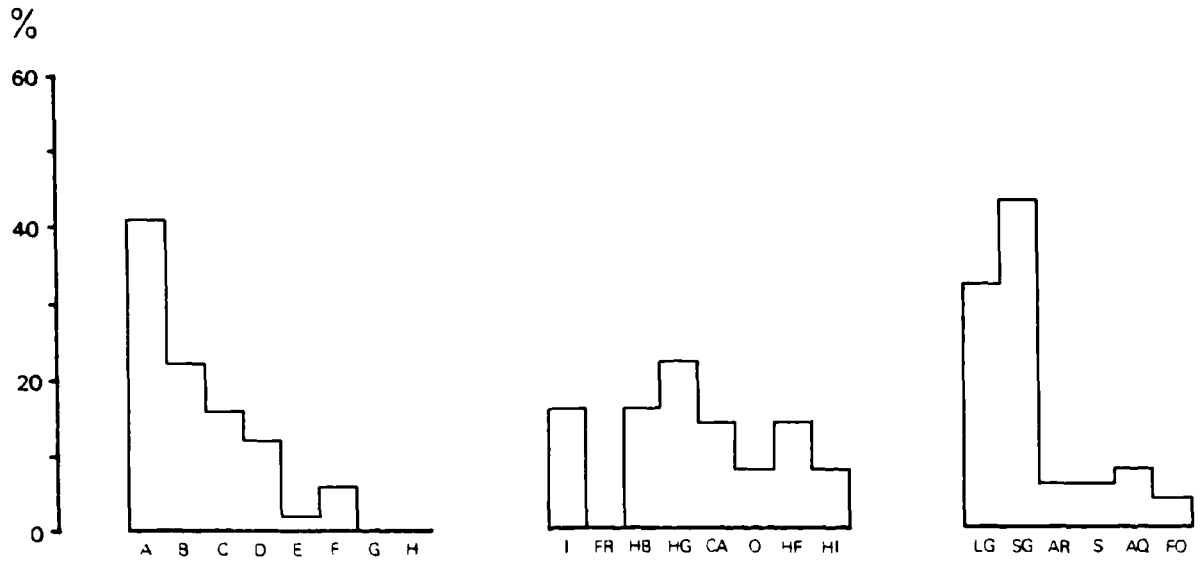
Size range: 24 - 25 species.

Mean size: 24·5 species.

Number of communities: 2.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 40·0 - 41·7 | 40·9 | 10 | 10·0 |
| B | 20·0 - 25·0 | 22·5 | 5 - 6 | 5·5 |
| C | 16·0 - 16·7 | 16·4 | 4 | 4·0 |
| D | 12·0 - 12·5 | 12·3 | 3 | 3·0 |
| E | 0·0 - 4·0 | 2·0 | 0 - 1 | 0·5 |
| F | 4·2 - 8·0 | 6·1 | 1 - 2 | 1·5 |
| G | 0·0 | 0·0 | 0 | 0·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 16·0 - 16·7 | 16·4 | 4 | 4·0 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 12·5 - 20·0 | 16·3 | 3 - 5 | 4·0 |
| HG | 20·8 - 24·0 | 22·4 | 5 - 6 | 5·5 |
| CA | 12·0 - 16·7 | 14·4 | 3 - 4 | 3·5 |
| O | 8·0 - 8·3 | 8·2 | 2 | 2·0 |
| HF | 12·0 - 16·7 | 14·4 | 3 - 4 | 3·5 |
| HI | 8·0 - 8·3 | 8·1 | 2 | 2·0 |
| Locomotor classes | | | | |
| LG | 29·2 - 36·0 | 32·6 | 7 - 9 | 8·0 |
| SG | 36·0 - 50·0 | 43·0 | 9 - 12 | 10·5 |
| AR | 4·2 - 8·0 | 6·1 | 1 - 2 | 1·5 |
| S | 4·0 - 8·3 | 6·1 | 1 - 2 | 1·5 |
| AQ | 4·2 - 12·0 | 8·1 | 1 - 3 | 2·0 |
| FO | 4·0 - 4·2 | 4·1 | 1 | 1·0 |

Figure 4.15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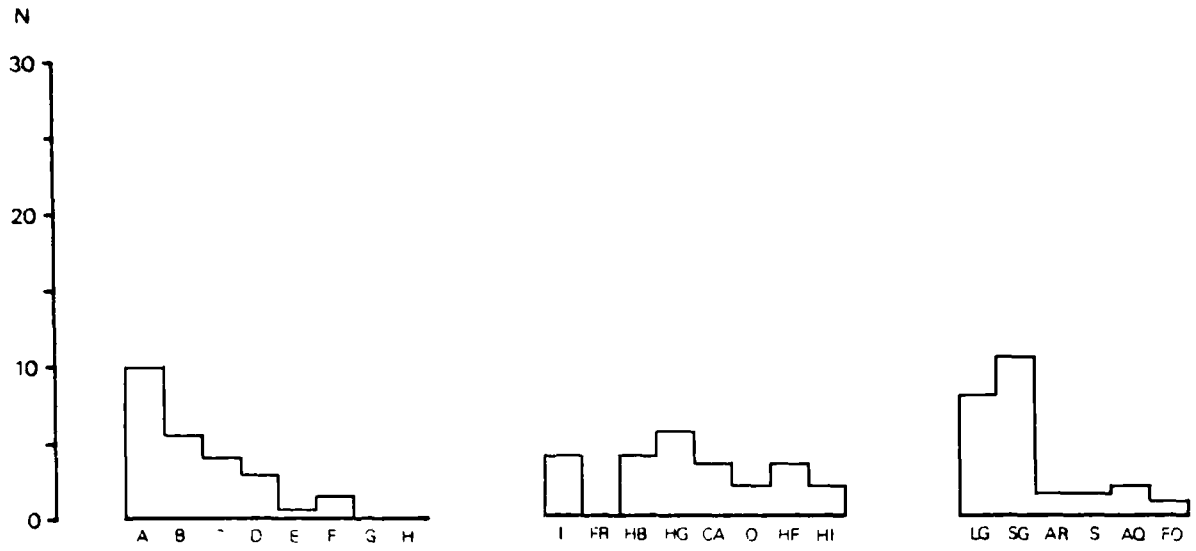
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b. Boreal Forest.

i Habitat and environment.

Subarctic, subalpine, needle-leaved coniferous forest stretches as a broad belt across North America and Europe between tundra in the north and deciduous forest or grassland to the south. Boreal forest (or "taiga") is supported in the region where conditions are more favourable than in the tundra (where trees cannot grow), but where summers are still too short and the winters too long to support deciduous broadleaf trees. This coniferous formation occupies the cold edge of the climatic range of forests and in many regions it is very wild and scarcely penetrable. The major dominants are needle-leaved evergreen conifers such as spruce, fir and pine (Eyre, 1968).

Seasonal periodicity in the boreal region can be extreme. The climate is generally cold and wet with a short growing season of 1 to 3 months and a mean temperature of less than 10°C. During more than six months of the year the mean temperature is less than 0°C, and maximum summer temperatures are usually about 20°C to 23°C, while in winter temperatures may drop as low as -50°C. Annual precipitation is between 10 and 40 inches, although nearly all the boreal forest has a mean annual rainfall of less than 40 inches, and most of the formation is found between the 15 and 20 inch isohyets

(Money, 1965; Walter, 1973). Most of the rainfall is concentrated during the summer and since precipitation exceeds potential evaporation, the boreal zone has a positive water balance and is classed as a humid region. The ground is continuously frozen during winter but snow cover is normally shallow. Dominance is often markedly affected by local conditions, but low floristic richness of both the understory and tree layers is almost universally characteristic. In some places stands may be almost pure, and the dense shade cast by closely packed evergreens drastically impairs the development of understory shrubs and herbs. The true boreal zone commences where the climate becomes unfavourable for broadleaf species, but seral stages involving deciduous broadleaves show clearly that this life-form is not totally excluded by environmental conditions.
The absence of broadleaf species from mature stands appears to be a result of the competitive superiority of shallow-rooted, fast-growing, evergreen conifers whose physiology is more suited to the climate of the region.

The needles of coniferous evergreens reduce winter water-loss to very low levels, which means that evergreens do not lose the first part of the growing season to leaf development. Unlike deciduous trees, evergreens are able to photosynthesise as soon as conditions become favourable, making them well suited to areas with cold winters and a short growing season.

Only under the most rigorous conditions are evergreens unable to survive. In the most northern areas of the boreal forest the winter climate is so harsh that no tree which carries its leaves through the winter is likely to survive. In these areas slow-growing deciduous trees tend to be dominant and deciduous birches, aspens and larches often survive on the edge of the tundra beyond the limit of evergreen tree growth. In both the Nearctic and the Palaearctic the forest-tundra boundary lies farther north in western areas where the climate is moderated by warm westerly winds. At this northern limit trees are stunted and dispersed and the forest appears to fade into tundra. Open areas in the forest tundra are usually occupied by dwarf-shrub tundra. In places the transition from boreal forest to treeless tundra is a mosaic where local relief allows outliers of forest to survive surrounded by tundra (Money, 1965). The southern ecotones take the form of mosaic associations of neighbouring vegetation types giving rise to the mixed forests of Europe and the (boreal) forest-steppe of the central Siberian plain.

ii Ecological diversity of mammal communities.

The boreal forest sample consists of 14 geographical communities compiled from distribution maps. Table 4.14 summarizes the ecological diversity of these communities. The mean proportion of the community and

number of species in each adaptational class are shown in figure 4.16.

The species richness indicates that the productivity of boreal forest is less than that of temperate deciduous forest. A large proportion of the species present in these communities have body weights of less than 10kg. and frequently at least 75% of the community falls in this range. The overall pattern is similar to that of tundra (figures 4.17 and 4.18), although the species richness of boreal forest communities is usually considerably greater than that of tundra communities.

Carnivores constitute the most numerous dietary class, followed by grazers and insectivores. There is usually a number of browsers, herbivore-frugivores, herbivore-insectivores and omnivores also present. Food sources with a high energy yield are apparently less abundant than in deciduous forest. The pattern is similar to that for tundra communities although the larger size of boreal forest communities and the more frequent occurrence of dietary classes such as browsers, herbivore-frugivores, herbivore-insectivores and omnivores argues for a habitat that is not only more productive than tundra but also presents a wider range of edible resources.

The locomotor pattern is dominated by ground adapted mammals. Arboreal and fossorial forms are less common than in deciduous forest and in many areas fossorial forms are precluded altogether by permafrost. The smaller number of arboreal forms could arise as a result of a less complex physical structure, but it seems likely that there is also a narrower range of resources available to arboreal species than in deciduous forest. The overall pattern has similarities to that for deciduous forest but the community structure suggests that boreal forest is less productive, less diverse and more seasonal.

Table 4.14 & Figure 4.16.

Ecological diversity of geographical communities from temperate boreal forest.

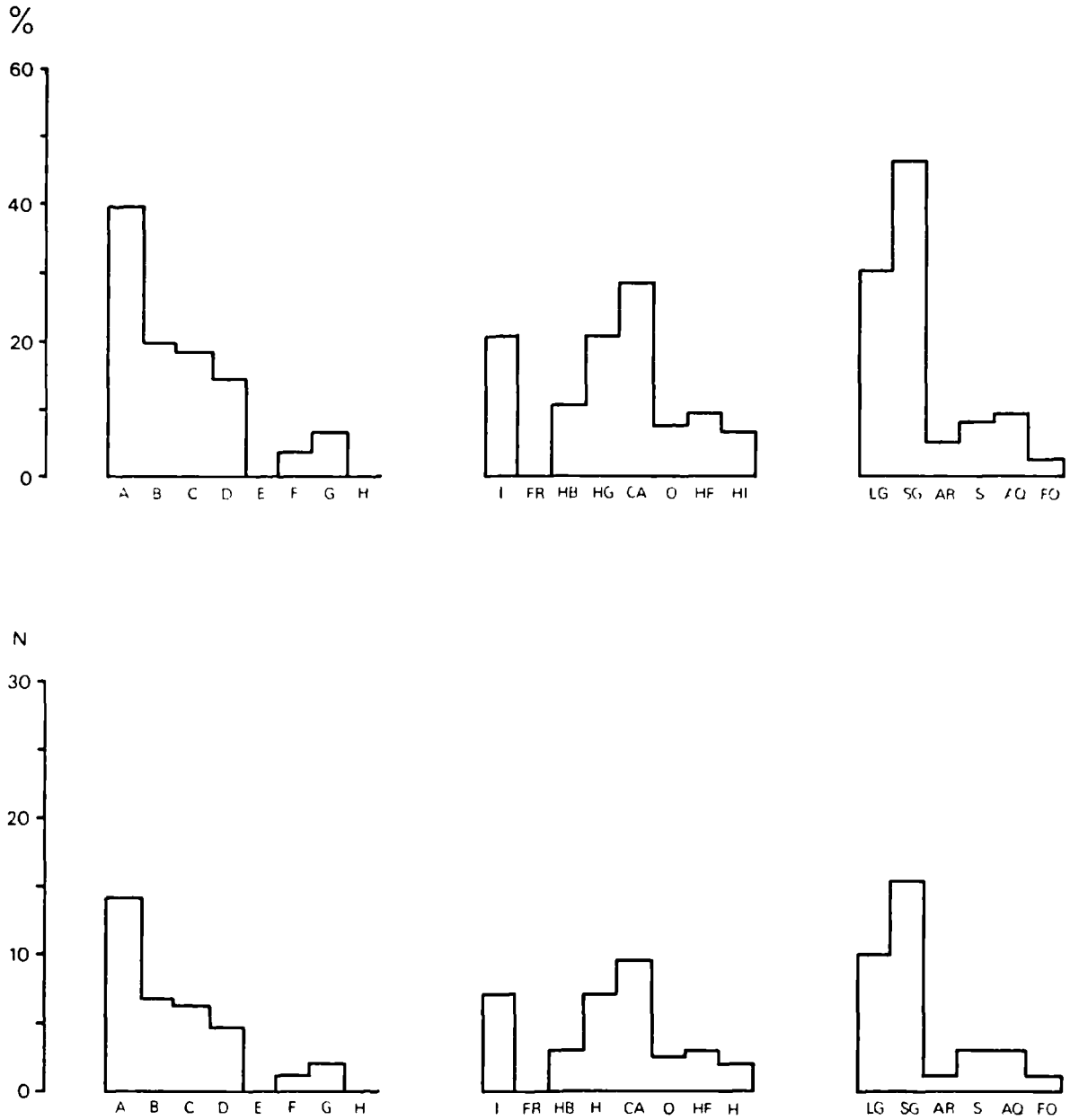
Size range: 22 - 44 species.

Mean size: 34·4 species.

Number of communities: 14.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 27·3 - 48·8 | 39·4 | 6 - 21 | 13·9 |
| B | 15·4 - 21·9 | 19·4 | 4 - 9 | 6·7 |
| C | 12·9 - 23·1 | 18·0 | 4 - 8 | 6·1 |
| D | 11·4 - 18·2 | 13·8 | 4 - 5 | 4·6 |
| E | 0·0 2·3 | 0·2 | 0 - 1 | 0·1 |
| F | 0·0 - 9·1 | 3·2 | 0 - 2 | 1·0 |
| G | 2·3 - 9·1 | 5·9 | 1 - 2 | 1·9 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 12·9 - 28·6 | 20·1 | 4 - 10 | 6·9 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 4·9 - 18·2 | 9·9 | 2 - 5 | 3·2 |
| HG | 9·1 - 26·8 | 19·9 | 2 - 11 | 7·0 |
| CA | 20·9 - 36·4 | 28·1 | 8 - 13 | 9·5 |
| O | 3·6 - 9·8 | 7·0 | 1 - 4 | 2·5 |
| HF | 6·3 - 16·3 | 9·2 | 2 - 7 | 3·2 |
| HI | 2·9 - 9·1 | 5·8 | 1 - 4 | 2·1 |
| Locomotor classes | | | | |
| LG | 23·3 - 45·5 | 29·8 | 9 - 12 | 9·9 |
| SG | 36·4 - 50·0 | 45·7 | 8 - 20 | 15·8 |
| AR | 2·9 - 9·3 | 5·2 | 1 - 4 | 1·9 |
| S | 4·7 - 11·5 | 8·5 | 2 - 4 | 2·9 |
| AQ | 4·5 - 13·5 | 9·1 | 1 - 5 | 3·3 |
| FO | 0·0 - 3·2 | 1·7 | 0 - 2 | 0·8 |

Figure 4.16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c. Tundra.

i Habitat and environment.

The term "tundra" is usually applied to all types of vegetation in the treeless arctic. The circum-arctic tundra is a single formation which occurs in Eurasia and North America. However, even within this formation, differences in life-form and general appearance can readily be observed. Tundra vegetation occurs in regions beyond the timberline which have cold, usually moist climates with short growing seasons. The main factors limiting plant growth in the tundra are the severity of the winter months and the shortness of the summer growing season. The productivity of the tundra is correspondingly low (see table 4.2).

Tundra regions beyond the limit of tree growth experience an extremely harsh climate. It is "winter" for 10 to 12 months of the year and the average temperature of the warmest month is less than 10°C. Furthermore, there are rarely more than 50 frost-free days a year with a brief summer vegetative period averaging about 50 to 90 days but as little as 1 to 4 weeks in the harshest areas. At most there are no more than 188 days per year with a mean temp above 0°C, and there are sometimes as few as 55 (Walter, 1973). Most of these treeless arctic plains are underlain by

permafrost and the growth of plants depends on the depth to which the soil layer thaws during the summer growing season and, on average, only the top 18 inches of soil thaws in summer. In winter the average temperature is less than -50°C and this is often combined with winds of up to 60mph.. The summer growing season is notable for its long photoperiods which have given rise to the name "land of the midnight sun".

Precipitation in tundra areas is low and falls mainly as snow during the winter months. Snow cover can last as long as 7 to 8 months although it is usually shallow and often incomplete. Tundra areas have a positive water balance due to the low evaporation potential, but permafrost, combined with strong winter winds, exerts severe physiological drought on plants during winter months which appears to be a more critical factor limiting plant growth than low temperatures alone. Relatively few plant spe ies have developed tolerance to the rigorous conditions of the tundra, for instance, the tundra of North America supports about 600 species (which is approximately 3% of world angiosperms). Several different association types can be identified in the treeless arctic tundras depending on local conditions. Flowering herbaceous plants (particularly grasses and sedges) are almost universal. Dwarf shrubs, mosses and lichens compete successfully in most places. At its most luxuriant, 100% ground cover is acheived but

about 80% of plant biomass is below ground (corresponding to a root:shoot ratio of 4:1). Nearly complete ground cover is achieved in southerly areas near forests but in other areas the vegetation cover can be so sparse that the ground is almost bare. Drier soils support pure lichen tundra, whereas moister areas support mosses. In general the separate or collective effects of frost, winter winds, permafrost and a short growing season precludes the growth of trees and most of the vegetation is low, often only 10 cm. tall, dominated by perennial forbs, grasses, sedges, dwarf shrubs, mosses and lichens (Eyre, 1968; Money, 1965).

It seems that not all tundra communities are true climax, a condition which is dominated by grasses and sedges with lichen and moss understory (Eyre, 1968). Where grass and sedge species are less important, dominance is assumed by foliose lichens and mosses. Along with the main dominants are often found plants more usually associated with the woodlands and meadows of middle latitudes and high altitudes. Dwarf shrubs also occur sporadically and these may form arctic scrub communities which are found on sheltered slopes, particularly where the soil thaws deeply in summer and is rich and moist. It is thought that such communities are probably ecotones with the early seral stages of forest (Eyre, 1968). In arctic scrub a bushy growth is attained which may reach a height of several feet

although in arctic heath the species are low growing and do not reach this height. Tundra bogs and moors are not true climax communities, but are edaphic climaxes which occupy ill-drained localities within the boreal region.

ii Ecological diversity of mammal communities.

The sample of tundra communities consists of 9 geographical and 6 ecological communities. The comparability of these two sets of communities was discussed above (see p.169). Tables 4.15 and 4.16 show the ranges and means of the number of species and the proportion of the total community in each class of the ecological diversity distributions. Figures 4.17 and 4.18 show the mean values for each type of community plotted as ecological diversity histograms. The species richness of complete communities varies from 10 to 27 but even the largest tundra communities are comparatively small which indicates that tundra is a habitat of low productivity.

The weight distribution is strongly dominated by small bodied species, up to 60% may be less than 100g in body weight and there is always at least 50% of the community less than 1kg body weight. Normally 80% weigh less than 10kg with very few species greater than 10kg body weight. A habitat of low productivity such as this can only support a small biomass and the theory of r and K selection would suggest that in a harsh and unstable

habitat such as the tundra, small bodied r-selected species would tend to dominate. More simply, the tundra is not sufficiently productive year-round to support large populations of large-bodied species.

Dietary classes are dominated by carnivores and grazers. The third most abundant class are insectivores and small numbers of browsers, herbivore-frugivores, herbivore-insectivores and omnivores are usually present as well. Food sources with a relatively high energy yield might be important in supporting small-bodied species, but dietary classes adapted to the exploitation of high energy foods are not dominant and low energy food sources would therefore appear to be the most abundant.

The most common locomotor type is the small ground adapted mammal which corresponds with the preponderance of species of low body weight. Most of the remaining species are large ground adapted types. The abundance of ground adapated species indicates a general lack of structural complexity in the habitat, notably a lack of trees which occur sporadically in ecotonal areas of forest tundra whose communities contain one or two scansori l species. Trees are entirely absent from high tundra and communities from these area are completely dominated by ground adapted species.

Table 4.15 & Figure 4.17.

Ecological diversity of geographical communities from tundra.

Size range: 13 - 27 species.

Mean size: 22·2 species.

Number of communities: 9.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 37·0 - 52·2 | 45·7 | 6 - 12 | 10·1 |
| B | 9·1 - 21·7 | 16·2 | 2 - 5 | 3·7 |
| C | 12·0 - 22·7 | 16·2 | 2 - 5 | 3·6 |
| D | 8·7 - 15·4 | 12·6 | 2 - 4 | 2·8 |
| E | 0·0 | 0·0 | 0 | 0·0 |
| F | 3·8 - 8·0 | 5·6 | 1 - 2 | 1·2 |
| G | 0·0 - 8·3 | 3·6 | 0 - 2 | 0·9 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 15·4 - 22·7 | 19·8 | 2 - 5 | 4·4 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 4·3 - 14·8 | 8·7 | 1 - 4 | 2·0 |
| HG | 25·0 - 43·5 | 32·9 | 5 - 10 | 7·2 |
| CA | 21·7 - 40·0 | 30·5 | 5 - 8 | 6·6 |
| O | 0·0 - 4·5 | 2·2 | 0 - 1 | 0·6 |
| HF | 0·0 - 4·5 | 3·2 | 0 - 1 | 0·8 |
| HI | 0·0 - 4·3 | 2·7 | 0 - 1 | 0·7 |
| locomotor classes | | | | |
| LG | 21·7 - 40·0 | 34·4 | 5 - 10 | 7·6 |
| SG | 44·4 - 65·2 | 56·5 | 8 - 16 | 12·4 |
| AR | 0·0 | 0·0 | 0 | 0·0 |
| S | 0·0 - 12·5 | 6·7 | 0 - 3 | 1·7 |
| AQ | 0·0 - 9·1 | 2·3 | 0 - 2 | 0·6 |
| FO | 0·0 | 0·0 | 0 | 0·0 |

Figure 4.17

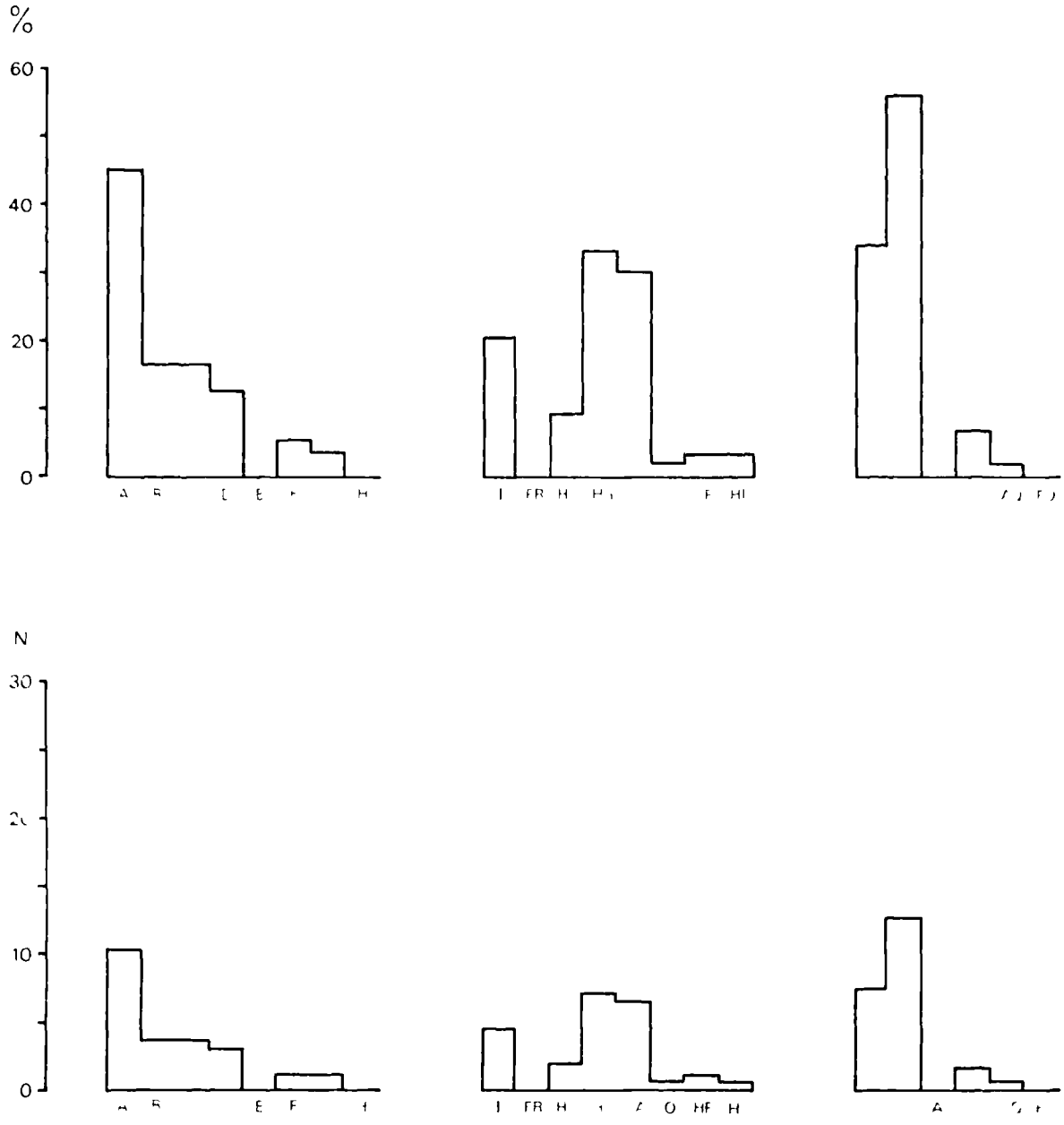


Table 4.16 & Figure 4.18.

Ecological diversity of ecological communities from tundra.

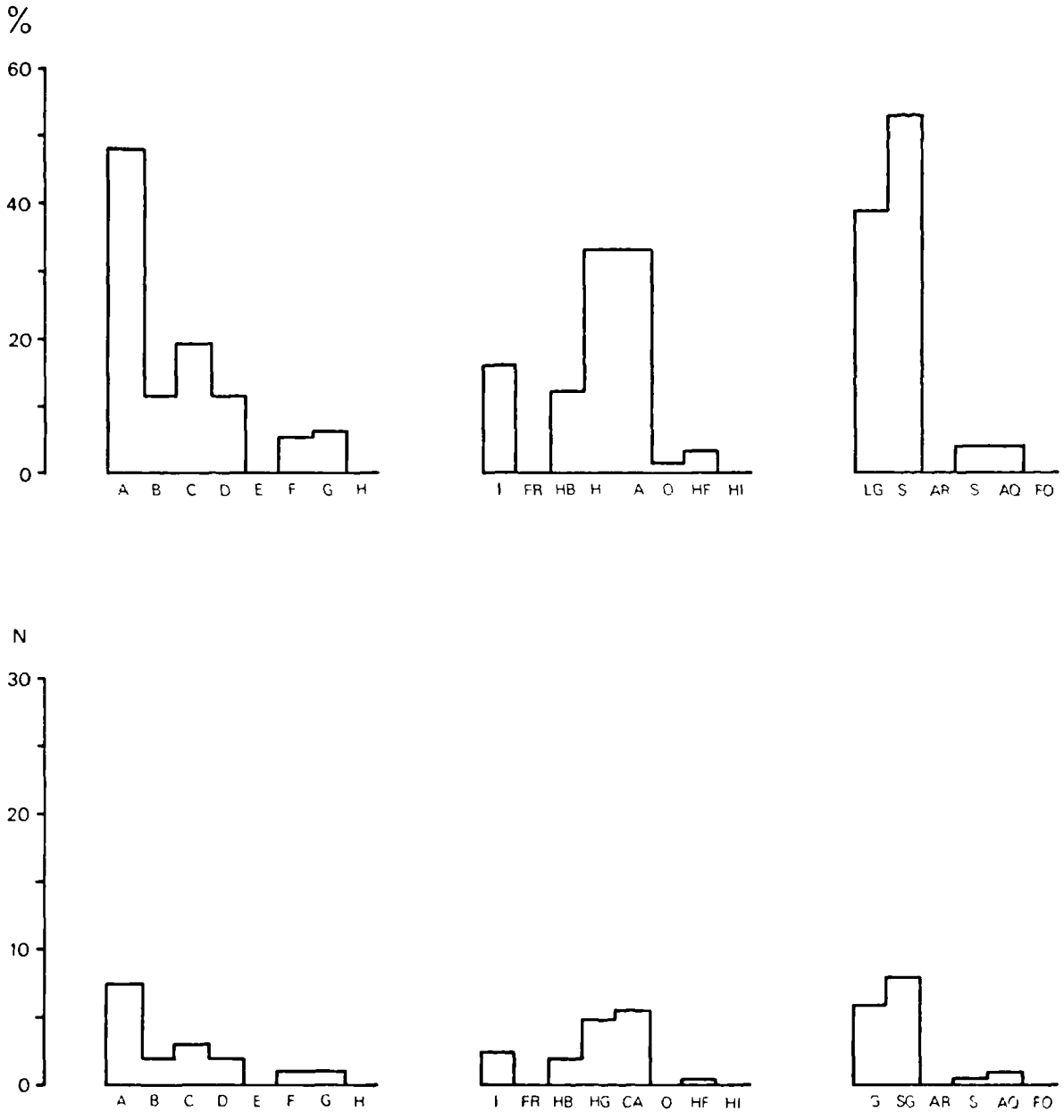
Size range: 10 -24 species.

Mean size: 15·8 species.

Number of communities: 6.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 41·7 - 60·0 | 47·8 | 5 - 10 | 7·3 |
| B | 0·0 - 18·2 | 10·9 | 0 - 3 | 1·8 |
| C | 14·3 - 21·4 | 19·1 | 2 - 5 | 3·0 |
| D | 6·7 - 19·0 | 10·7 | 1 - 4 | 1·8 |
| E | 0·0 | 0·0 | 0 | 0·0 |
| F | 0·0 - 10·0 | 5·5 | 0 - 1 | 0·8 |
| G | 0·0 - 9·1 | 6·0 | 0 - 2 | 1·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 13·3 - 20·0 | 16·1 | 2 - 4 | 2·5 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 8·3 - 19·0 | 12·3 | 1 - 4 | 2·0 |
| HG | 27·3 - 40·0 | 33·1 | 3 - 7 | 5·2 |
| CA | 27·3 - 37·5 | 32·9 | 4 - 9 | 5·7 |
| O | 0·0 - 4·2 | 0·7 | 0 - 1 | 0·2 |
| HF | 0·0 - 9·1 | 3·3 | 0 - 1 | 0·5 |
| HI | 0·0 | 0·0 | 0 | 0·0 |
| Locomotor classes | | | | |
| LG | 36·4 - 42·9 | 39·1 | 4 - 9 | 6·2 |
| SG | 45·8 - 60·0 | 53·0 | 6 - 11 | 8·2 |
| AR | 0·0 | 0·0 | 0 | 0·0 |
| S | 0·0 - 9·1 | 4·0 | 0 - 2 | 0·7 |
| AQ | 0·0 - 14·3 | 3·9 | 0 - 3 | 0·8 |
| FO | 0·0 | 0·0 | 0 | 0·0 |

Figure 4.18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G SG AR S AQ FO

d. Temperate grasslands (steppe).

i Habitat and environment.

Temperate grassland and steppe are found at similar latitudes to those occupied by deciduous forest. Deciduous forest formations are usually restricted to areas of oceanic climate where there are no sharp extremes of temperature and rainfall is more or less evenly distributed throughout the year, often with a summer maximum, whereas grasslands occur where rainfall is too low to support forest, but is higher than that which results in semidesert or true desert habitats. In the Palaearctic region steppe occurs in areas of continental climate where there is a greater seasonal amplitude of temperature (hotter summers and colder winters) with a lower annual mean. The annual mean rainfall also tends to be less and during the summer months evaporation exceeds rainfall and there is a negative water balance.

The temperate grasslands of the Palaearctic stretch from the mouth of the Danube across eastern Europe and Asia almost as far as the Yellow Sea (Eyre, 1968; Walter, 1973). The degree of aridity varies considerably and in general the forest-steppe boundary coincides with that between humid regions where rainfall exceeds evaporation potential and arid regions where evaporation exceeds rainfall (Walter, 1973).

The forest zone has no strongly marked dry period, whereas the steppe region normally has a period of drought in the late summer. The ecotone is intermediate in having a distinct dry period usually at some time during the summer months.

The vegetational season of steppe plants is limited by a cold winter and a late summer drought. There is a period of only about 4 months in late spring and early summer when sufficiently high temperatures combine with a sufficiently abundant rainfall to produce suitable growing conditions, however, productivity is high during this period (see table 4.2 and Walter, 1973). The below-ground phytomass far exceeds that above ground and during the growing season plants of steppic regions are able to store enough nutrients to survive non-productive seasons. Naturally occuring steppes and grasslands are found chiefly in continental interiors where annual rainfall is between 10 and 30 inches per year. In these regions grasses predominate although there is wide variation in the genera and species present. Meadow-steppes are composed predominantly of sod-forming grasses with subordinate tussock grasses which may grow luxuriantly to reach a height of four feet while a small but consistently present part of the flora in climax grasslands is formed by forbs, especially broad-leaved herbs (Eyre, 1968).
The shallow root systems of all these species allow

them to survive where tree seedlings would die. The forest-steppe ecotone is not an homogenous vegetation type but is a mosaic of forest and meadow steppe. Relief, soil type and climate determine the dominant type of vegetation in this mosaic. With an increase in drought, species richness decreases towards semi-desert and desert conditions in the deep continental interiors. Like the deciduous forest, grasslands have been substantially altered by the activities of man (mainly by cultivation and grazing) and it is unlikely that many areas of unaltered climatic climax still exist.

ii Ecological diversity of mammal communities.

The sample of steppe communities consists of four geographical communities whose species richness ranges from 36 to 47 suggesting an environment of moderate productivity similar to that of deciduous forest. The ecological diversity of these communities is summarized in table 4.17 and mean values for each ecological diversity class are plotted in figure 4.19.

The weight distribution of steppe communities is most similar to that of deciduous forest. These two types of community are also very similar in overall species richness. The diet distribution is dominated by grazers while the locomotor distribution is dominated by ground adpated mammals. Carnivores are the second most

abundant dietary class and there are never more than one or two browsers. The presence of herbivore-frugivores, herbivore-insectivores and omnivores indicates that although grasses predominate, other resources are present in sufficient abundance to support non-grazing species. The presence of fossorial species suggests light, fairly well drained soil conditions and an absence of permafrost, waterlogging and extensive woody root systems.

The size of steppe communities apparently relates to the fact that although steppe is seasonal, its carrying capacity even during the harshest months is sufficient to support a commnity of moderate size, in contrast to boreal forest and tundra where seasonality places a severe constraint on the plant and animal communities. The dominance of grazers reflects the fact that the resource base for primary consumers consists largely of grasses and low herbage. The predominance of ground adapted species indicates the lack of structural complexity in the habitat. One or two arboreal and scansorial species are found in areas where trees are present.

The overall indication of this ecological diversity pattern is a habitat of moderate carrying capacity, whose resource base consists mainly of grasses.

There are few trees which leads to low structural complexity. The environment is fairly productive and apparently less seasonal than tundra and boreal forest.

Table 4.17 & Figure 4.19.

Ecological diversity of geographical communities from steppe.

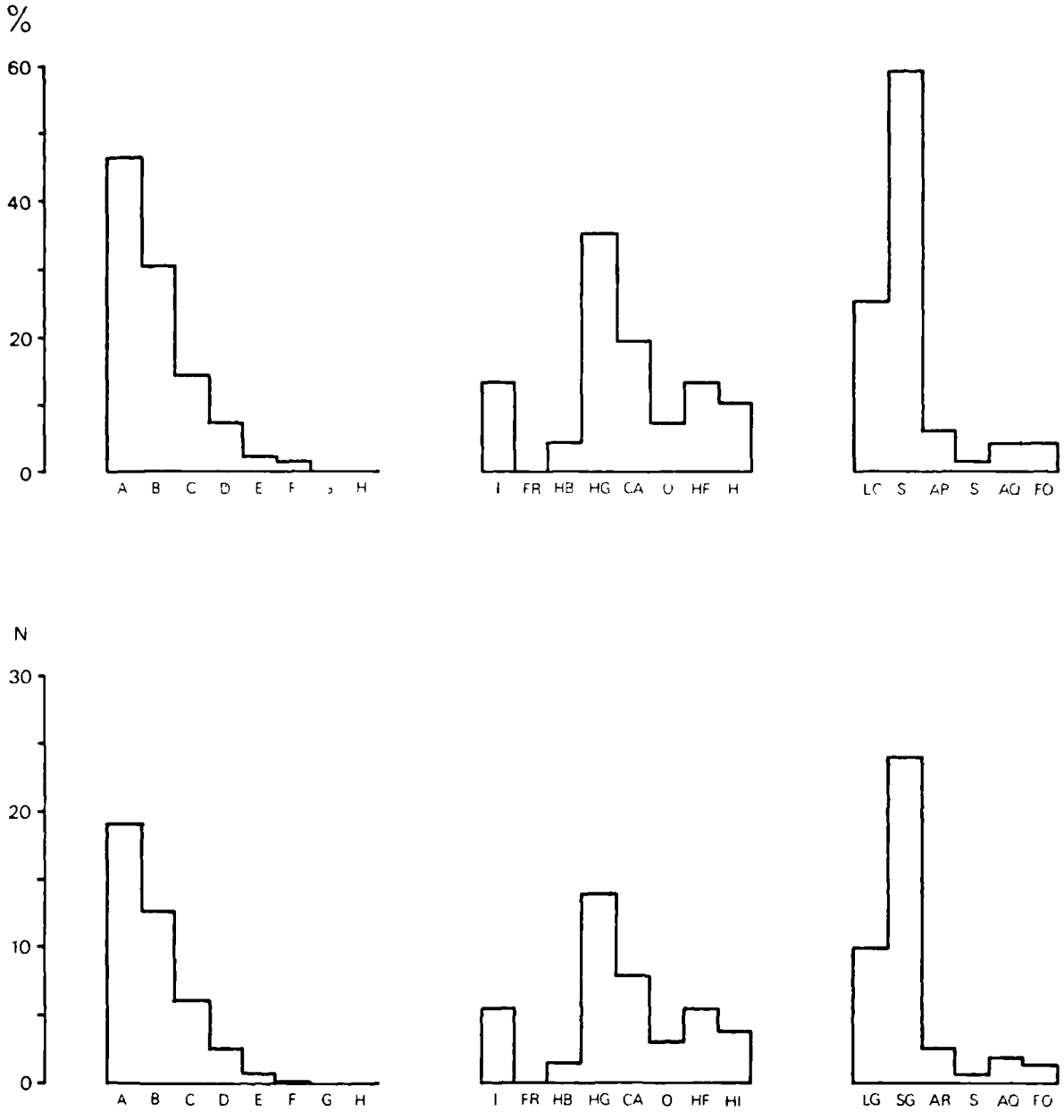
Size range: 35 - 47 species.

Mean size: 40·0 species.

Number of communities: 5.

| | % range | % mean | N raNGE | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 44·4 - 46·8 | 45·9 | 16 - 22 | 18·4 |
| B | 29·8 - 31·4 | 30·6 | 11 - 14 | 12·2 |
| C | 11·4 - 16·3 | 13·9 | 4 - 7 | 5·6 |
| D | 4·7 - 8·6 | 7·1 | 2 - 3 | 2·8 |
| E | 0·0 - 2·9 | 2·1 | 0 - 1 | 0·8 |
| F | 0·0 - 2·3 | 0·5 | 0 - 1 | 0·2 |
| G | 0·0 | 0·0 | 0 | 0·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 2·9 - 14·9 | 10·7 | 1 - 7 | 4·4 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 2·6 - 4·7 | 3·5 | 1 - 2 | 1·4 |
| HG | 25·5 - 41·0 | 34·2 | 11 - 16 | 13·6 |
| CA | 15·4 - 22·9 | 19·4 | 6 - 10 | 7·8 |
| O | 4·7 - 8·6 | 7·6 | 2 - 4 | 3·0 |
| HF | 11·1 - 14·9 | 13·5 | 4 - 7 | 5·4 |
| HI | 7·0 - 17·1 | 11·2 | 3 - 6 | 4·4 |
| Locomotor classes | | | | |
| LG | 19·1 - 30·8 | 25·4 | 9 - 12 | 10·0 |
| SG | 55·3 - 62·9 | 59·8 | 22 26 | 23·8 |
| AR | 4·7 - 8·5 | 5·9 | 2 - 4 | 2·4 |
| S | 0·0 - 2·3 | 0·9 | 0 - 1 | 0·4 |
| AQ | 0·0 - 10·6 | 3·5 | 0 - 5 | 1·6 |
| FO | 2·6 - 7·0 | 3·5 | 1 - 3 | 1·8 |

Figure 4.19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A B C D E F G H
I FR HB HG CA O HF HI
LG SG AR S AQ FO
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A B C D E F G H
I FR HB HG CA O HF HI
LG SG AR S AQ FO

e. Semidesert and Desert.

i Habitat and environment.

There appears to be no systematic description of the semidesert formations of Eurasia as a whole (Eyre, 1968). These deserts and semideserts presently cover the vast area from the plains east of the Caspian sea to the Great Khingan Mountains on the eastern edge of the Gobi Desert (Eyre, 1968). In general, deserts and semideserts tend to occur in the hearts of the continents where little moist air penetrates, with the result that rainfall is slight and irregular. In central Asia the humidity may be as low as 20%. These areas differ from low latitude deserts in having a cold season and in many areas winter is bitterly cold. In contrast the summers tend to range from very warm to hot. However, it is difficult to generalize because middle latitude arid and semi-arid climates occur through some 20 degrees of latitude in both Asia and North America, while topography varies from high plateaux to low inland basins (Money, 1968).

Semidesert is distinguishable from true desert by its diffuse vegetation and although ground cover is only about 25%, in the desert biome vegetation density is even lower than this and it is normally contracted or clumped rather than diffuse (Walter, 1973).

The nature of the plant cover in semidesert varies greatly. In the frost-free subtropics and in the tropics, the plant cover consists mainly of woody plants and succulents. In the temperate zone where cold winters are the rule, these are mainly dwarf shrubs, especially of the genus Artemisia, although sclerophyllous grasses are also present (Walter, 1973). Herbaceous plants are of much greater frequency in the Eurasian formations than in the deserts and semideserts of North America, and grasses in particular are much more important. Where rainfall is above average, isolated trees may occur, and with further increases in rainfall thin stands of trees appear which finally lead to schlerophyllous woodlands.

The ecotone between semi-desert and desert is not always clearly defined, but generally it is to be found in the zone where increasing (usually winter) rains lead to the replacement of the contracted desert vegetation by the diffuse vegetation typical of semideserts (Walter, 1973). True deserts are primarily subtropical, but in most cases they are continuous with areas of warm semidesert scrubland. They generally occur in regions having an annual rainfall of less than 10 inches (or perhaps slightly more if it is very unevenly distributed). The true deserts are very poor in plant species. There are three forms of plants adapted to desert conditions, annuals which avoid

drought by growing only when there is sufficient moisture during brief wet periods, water storing succulents (such as cacti) and desert shrubs that have small thick leaves which can be shed during long periods of drought.

ii Ecological diversity of mammal communities.

The sample of semidesert and desert communities consists of 4 geographical communities from semidesert and 3 geographical communities from desert habitats. The species richness of the semidesert communities ranges between 24 and 30 species with a mean of 26.8. The species richness of the desert communities ranges between 6 and 19 with a mean of 10.7 species. The ecological diversity of these communities is summarized in tables 4.18 and 4.19 and figures 4.20 and 4.21.

The weight distribution of semidesert communities shows a relatively high proportion of species in the middle part of the body size range (classes B to E) which, combined with the low species richness, distinguishes semidesert from other community types. The dietary distribution is dominated by two diet classes; grazers and carnivores. There are no insectivores or frugivores present, but browsers, herbivore-frugivores, omnivores and herbivore-insectivores are consistently found in small numbers. The locomotor distribution is dominated

by ground adapted mammals which form a mean proportion of nearly 93% of this type of community. Aquatic, scansorial and fossorial mammals occur occasionally but there are no arboreal species.

The species richness of semidesert communities suggests a habitat of moderate to low productivity and the ecological diversity distributions suggest further that this is expressed largely in the type of vegetation on which grazers specialize. The relatively low number of small-bodied species shows that there is a paucity of high energy resources but the absence of large-bodied animals indicates that the habitat is not sufficiently productive to support viable breeding populations of large mammals. Dietary classes such as omnivores, herbivore-frugivores and herbivore-insectivores show that higher energy resources are present (perhaps seasonally) but not in sufficient abundance to support specialists such as frugivores and insectivores. The low number of browsers indicates a poverty of the bush and tree stratum to provide browse for this dietary class. Further weight is lent to this point by the overwhelming dominance of large and small ground adapted forms, the absence of arboreal species and the scarcity of scansorial species. Overall, the ecological diversity shows that semidesert is a habitat of moderate to low productivity with relatively low, perhaps seasonal, resource diversity and low structural complexity.

The ecological diversity of communities from desert habitats is difficult to interpret since the overwhelming feature is the low species richness. The weight distribution shows no distinctive patterns on which any strong inferences could be based. In the dietary distribution, an average of half the community consists of grazers, with carnivores the only other class consistently present in any but the smallest numbers. The locomotor distribution is clearly dominated by ground adapted forms.

The ecological diversity of desert communities seems to be a more extreme version of that described for semidesert communities. Overall, the pattern is indicative of a habitat of low productivity, with low resource diversity and low structural complexity.

Table 4.18 & Figure 4.20.

Ecological diversity of geographical communities from semidesert.

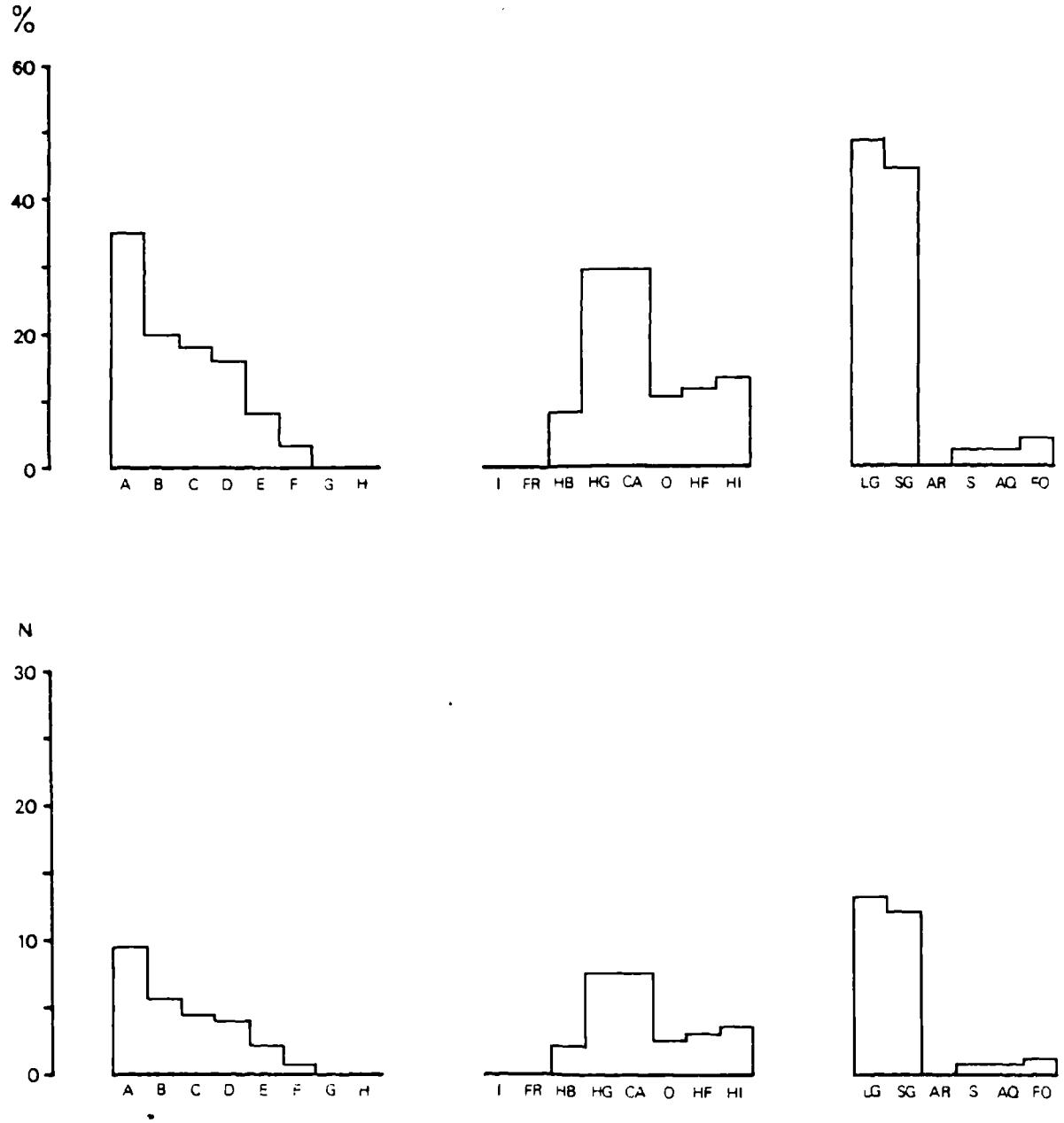
Size range: 24 - 30 species.

Mean size: 26·8 species.

Number of communities: 4.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 25·0 - 46·2 | 35·5 | 7 - 12 | 9·5 |
| B | 14·3 - 26·7 | 20·3 | 4 - 8 | 5·5 |
| C | 12·5 - 23·1 | 17·6 | 3 - 6 | 4·7 |
| D | 7·7 - 21·4 | 15·8 | 2 - 6 | 4·2 |
| E | 3·8 - 14·3 | 8·3 | 1 - 4 | 2·2 |
| F | 0·0 - 3·8 | 2·7 | 0 - 1 | 0·7 |
| G | 0·0 | 0·0 | 0 | 0·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 0·0 | 0·0 | 0 | 0·0 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 4·2 - 10·7 | 8·2 | 1 - 3 | 2·2 |
| HG | 17·9 - 34·6 | 28·7 | 5 - 10 | 7·7 |
| CA | 23·2 - 35·7 | 28·7 | 6 - 10 | 7·7 |
| O | 7·1 - 15·4 | 10·2 | 2 - 4 | 2·7 |
| HF | 3·8 - 20·8 | 11·3 | 1 - 5 | 3·0 |
| HI | 7·7 - 17·9 | 12·8 | 2 - 5 | 3·5 |
| Locomotor classes | | | | |
| LG | 43·3 - 57·7 | 48·3 | 11 - 15 | 13·0 |
| SG | 38·5 - 50·0 | 44·5 | 10 - 14 | 12·0 |
| AR | 0·0 | 0·0 | 0 | 0·0 |
| S | 0·0 - 3·6 | 1·7 | 0 - 1 | 0·5 |
| AQ | 0·0 - 3·6 | 1·7 | 0 - 1 | 0·5 |
| FO | 3·3 - 4·2 | 3·7 | 1 | 1·0 |

Figure 4.20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I FR HB HG CA O HF HI
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Table 4.19 & Figure 4.21.

Ecological diversity of geographical communities from desert.

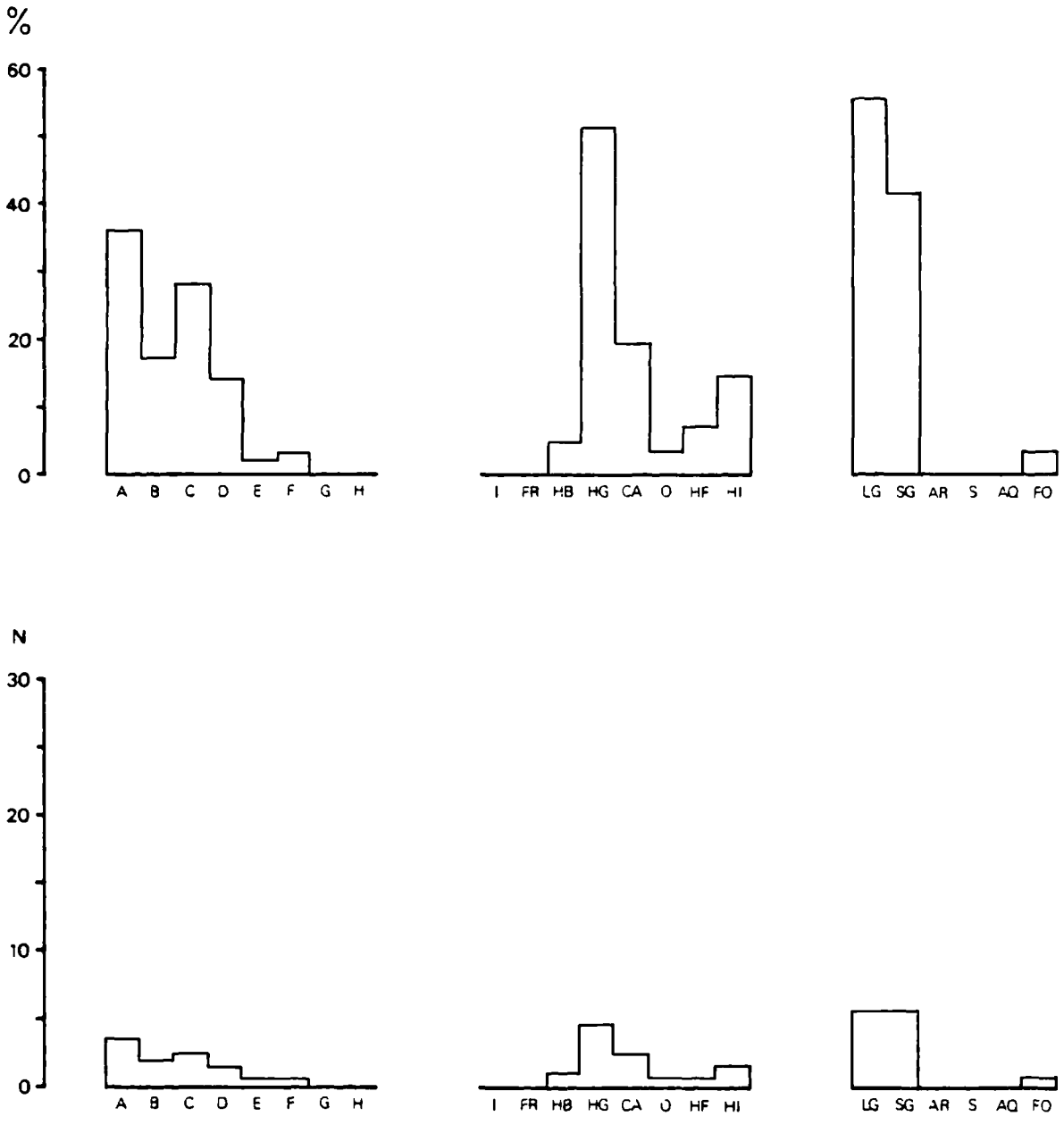
Size range: 6 - 19 species.

Mean size: 10·7 species.

Number of communities: 3.

| | % range | % mean | N range | N mean |
|---|---|---|---|---|
| Weight classes | | | | |
| A | 31·6 - 42·9 | 35·9 | 2 - 6 | 3·7 |
| B | 14·3 - 21·1 | 17·4 | 1 - 4 | 2·0 |
| C | 21·1 - 33·3 | 27·7 | 2 - 4 | 2·7 |
| D | 10·5 - 16·7 | 13·8 | 1 - 2 | 1·3 |
| E | 0·0 - 5·3 | 1·8 | 0 - 1 | 0·3 |
| F | 0·0 - 10·5 | 3·5 | 0 - 2 | 0·7 |
| G | 0·0 | 0·0 | 0 | 0·0 |
| H | 0·0 | 0·0 | 0 | 0·0 |
| Diet classes | | | | |
| I | 0·0 | 0·0 | 0 | 0·0 |
| FR | 0·0 | 0·0 | 0 | 0·0 |
| HB | 0·0 - 15·8 | 5·3 | 0 - 3 | 1·0 |
| HG | 31·6 - 71·4 | 51·0 | 3 - 6 | 4·7 |
| CA | 14·3 - 26·3 | 19·1 | 1 - 5 | 2·3 |
| O | 0·0 - 10·5 | 3·5 | 0 - 2 | 0·7 |
| HF | 0·0 - 16·7 | 7·3 | 0 - 1 | 0·7 |
| HI | 10·5 - 16·7 | 13·8 | 1 - 2 | 1·3 |
| Locomotor classes | | | | |
| LG | 42·1 - 66·7 | 55·3 | 4 - 8 | 5·3 |
| SG | 33·3 - 47·4 | 41·2 | 2 - 9 | 5·3 |
| AR | 0·0 | 0·0 | 0 | 0·0 |
| S | 0·0 | 0·0 | 0 | 0·0 |
| AQ | 0·0 | 0·0 | 0 | 0·0 |
| FO | 0·0 - 10·5 | 3·5 | 0 - 2 | 0·7 |

Figure 4.21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I FR HB HG CA O HF HI
LG SG AR S AQ FO

f. Alpine Formations.

There is a tendency in mountainous areas where altitude provides a series of contrasting environments for the vertical array of habitats encountered with increasing altitude to parallel the horizontal array found when passing from low to high latitudes.

Alpine tundra-like areas occur on high mountains in temperate regions beyond the altitudinal timber line. In general the vegetation is similar to high latitude tundra and although a large number of species are found only in one or the other, there are also many species common to both. There are thus great similarities in life-form and species content between arctic and alpine vegetation. Although winters are similar in both areas there are some important environmental differences associated mainly with summer climate. Alpine areas have higher precipitation but no permafrost, the maximum summer temperature is higher, and there is also a different photoperiod regime (the intensity of solar radiation is greater but there are not the same extremes of daylength). Alpine vegetation also experiences relatively high light intensity and daytime warming throughout the whole year. Except in sheltered places it also has to withstand high windspeeds. Because of these differences, physical drought is a more frequent hazard to alpine communities than it is in arctic tundra. However, the same adaptations that cope with the extreme

cold and physiological drought of arctic winters can cope with the extreme cold and high transpiration rates caused by the hot sun and drying winds of alpine areas.

Belts of coniferous forest are also found south of the boreal region in areas of moderate to high elevation and sometimes even in the tropics, although they occur mainly in mountain ranges of middle latitudes. These subalpine formations generally occur in zones that are 5°C warmer than the taiga with 20 to 50% greater precipitation (Barbour et al., 1980).
Temperature decreases with altitude but daytime temperatures during spring and autumn are higher and both light and heat are greater throughout the year in mountains than in boreal regions. Day length is longer in boreal forest in summer but shorter in winter. Most species of the subalpine formation are closely related to boreal forms but tend to be distinct.

g. The Palaearctic Set.

The comparative set of Palaearctic communities consists of 20 geographical communities whose associated climax habitats are listed in table 4.16. The single linkage dendrograms based on proportions and absolute numbers of species in each class of the ecological diversity distribution are shown in figure 4.22.

The modern Palaearctic set can be divided into 4 groups on the basis of proportions. The largest group consists of forest communities belonging to both deciduous and boreal forest habitats. A second group consists of two steppe communities and a third of the four tundra communities. The final group consists of semidesert communities, two of which are similar to each other while the other two do not appear to be closely related to any other community. Different groups are formed when absolute numbers are used. The first group consists of three boreal forest communities and the two largest tundra communities. Another group contains the four semidesert localities. The two smaller tundra localities associate closely with each other. A further group contains 3 boreal forest and 4 deciduous forest communities, and the last grouping consists of the two steppe communities.

Overall these dendrograms indicate that tundra communities share a similar pattern in terms of shape alone but when species richness is taken into account, the larger tundra communities are more similar to some boreal forest communities. Likewise, communities from deciduous forest habitats are similar to each other but also share basic similarities with boreal forest communities which leads to the formation of mixed subgroups. The two steppe communities have a distinctive pattern and the semidesert communities do not share a similar shape but do associate together when species richness is taken into account.

Table 4.20. Habitat types of communities in the modern temperate comparative set.

| Community number | Habitat type | Community type |
|---|---|---|
| 1 | Tundra | geographical |
| 2 | " | " |
| 7 | " | " |
| 8 | " | " |
| 11 | Boreal forest | " |
| 12 | " " | " |
| 13 | " " | " |
| 17 | " " | " |
| 18 | " " | " |
| 19 | " " | " |
| 23 | Deciduous forest | " |
| 24 | " " | " |
| 25 | " " | " |
| 26 | Forest-steppe | " |
| 28 | Steppe | " |
| 29 | " | " |
| 42 | Semidesert | " |
| 47 | " | " |
| 49 | " | " |
| 51 | " | " |

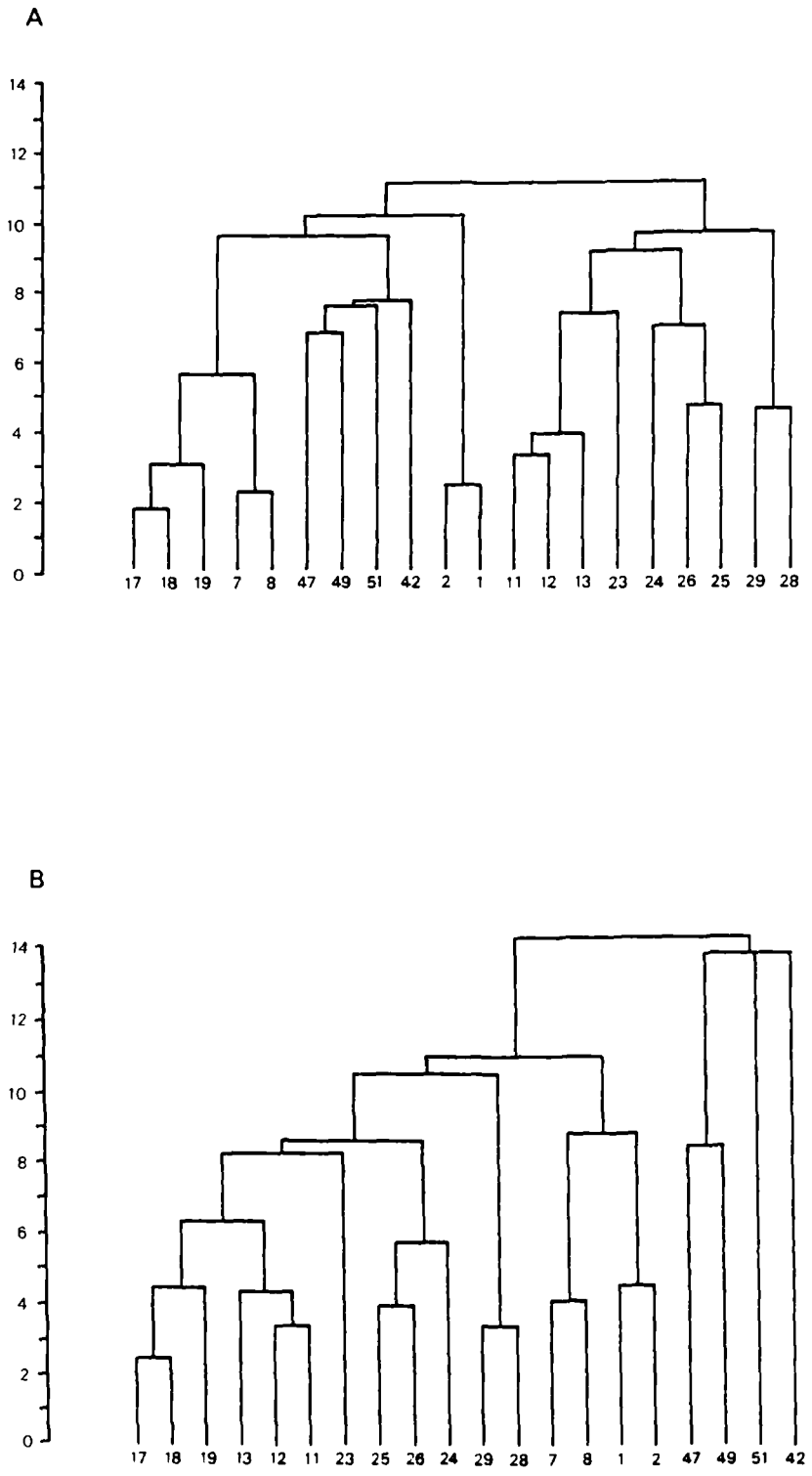
Figure 4.22. Single linkage dendrogram grouping of communities in the modern temperate comparative set.

A. Dendrogram based on N, the number of species in each class of the ecological diversity distribution.

B. Dendrogram based on %, the proportion of the community in each class of the ecological diversity distribution.

For a discussion of these dendrograms see the text (pp. 273-4). A summary of the habitats of the numbered communities is given in table 4.20 (p. 275).

Figure 4.22.


A
14
12
10
8
6
4
2
0
17 18 19 7 8 47 49 51 42 2 1 11 12 13 23 24 26 25 29 28
B
14
12
10
8
6
4
2
0
17 18 19 13 12 11 23 25 26 24 29 28 7 8 1 2 47 49 51 42

The groups used in residual diversity patterns based on the modern temperate sample are derived from the dendrograms shown in figure 4.22 and are as follows:

| Community number | Habitat type | Key |
|---|---|---|
| 1, 2, 7, 8. | Tundra |  |
| 11, 12, 13, 17, 18, 19. | Boreal forest |  |
| 23, 24, 25, 26, 28, 29. | Deciduous forest |  |
| 42,47, 49, 51. | Semidesert |  |

Chapter 4: Summary.

Chapter 4 explores the issue of how the structure of modern communities is related to characteristics of the habitats in which they live. It is shown that each habitat supports a community with a distinctive adaptational structure.

Two different methods of compiling faunal lists are described and two different types of community are defined. Ecological derive from field studies and collections, while geographical communities are obtained from distribution maps. Geographical and ecological communities from tundra and temperate deciduous forest are compared to show that these two types of community resemble each other in structure.

The relationship between environmental variables such as habitat structure and complexity, productivity and stability, and the adaptational structure of mammal communities is discussed. The ecological diversity of communities from modern tropical and temperate habitats is then described, together with an outline of the important features of each community and the way in which these relate to various characteristics of the habitat. It is also shown that communities can be grouped (by habitat type) by mathematical comparison of their Ecological Diversity and thus that each modern habitat is inhabited by a community with a distinctive adaptive structure.

# Chapter 5

## The effects of species loss on modern communities

## 1. Introduction.

Each of the modern habitats described in chapter 4 has a community with a distinctive ecological structure. The habitats of modern communities can, by and large, be identified by their ecological diversity, residual diversity and taxonomic habitat index patterns. Unfortunately, the interpretation of fossil faunas is not quite so straightforward. In analysing modern communities, differences in community adaptational structure have been related to differences between habitats (see chapter 3). This relatively simple model cannot be used for fossil assemblages because there are two sources of variation involved, firstly, ecological differences between habitats and secondly, biases that can be introduced anywhere along the hazardous road from death to publication. The first factor was dealt with in chapter 4 and it is the second source of variation that is discussed in this chapter.

Because fossilization is such a chancy process, it is highly unlikely that every individual member of a natural community, species population or social group will be preserved except under the most extreme or unusual circumstances. In many cases several or even most of the species forming a community will fail to be preserved and represented in a fossil assemblage. These taphonomic biases may result in faunas from similar habitats appearing to have strikingly different patterns,

while faunas from different habitats may appear to have similar structures. Ideally, it is preferable to use an unbiased fauna and where an assemblage is heavily biased it is better not to treat it as representative of a natural community and to use an indicator method rather than a diversity method. In this chapter the effects of taphonomic biases will be simulated by gradually removing species from modern communities and then illustrating the effects of this species loss on residual diversity and taxonomic habitat index patterns. These simulations will show how these two methods react under conditions of species loss and to what extent they can be used with fossil assemblages that represent incompletely preserved communities.

The taxonomic habitat index and residual diversity patterns of communities from 11 modern habitat types are described. Each of these communities is then subjected to patterns of species loss intended to parallel the kinds of taphonomic bias that commonly influence the processes involved in turning a living animal community into a fossil assemblage. Body size seems to be the most significant character (see p.107) and in these simulations, species have been removed non-randomly with respect to their ecological diversity body size classification. Species were removed 3 at-a-time and the simulations terminated when just 10 species remained. Two simulation series were performed; the first started with the removal

of species from the smallest body size class (A) and then progressed to successively larger size classes (B - H). The second simulation series involved the removal of large-bodied species, starting from the largest body size class (H) and proceeding to the smaller classes (G - A). THI and residual diversity patterns were recalculated for the remaining species each time 3 species were removed. The principle stages in each simulation series are shown in the figures that follow in the remainder of this chapter. These figures do not necessarily illustrate every stage in each series, but the patterns shown have been chosen to demonstrate the salient points of each series.

2. Taxonomic Habitat Index simulations.

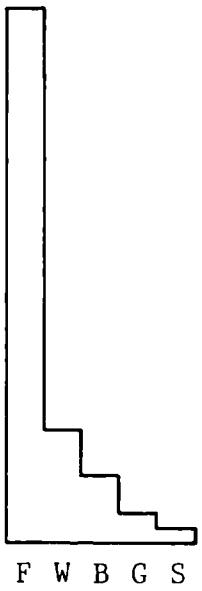
THI simulations were carried out for both tropical and temperate habitats. The simulations for tropical communities were carried out only at species level, while the temperate habitats are figured at both species and generic levels.

Each habitat is distinguished by a characteristic pattern which as a rule is marked by high values in one or perhaps two columns, while the other columns have variable but generally low values. The unbiased patterns are described first to demonstrate that habitats can be distinguished by the THI patterns of their communities before any species are lost. A community from each habitat type is then subjected to the two series of simulations; firstly, the removal of small-bodied species and secondly, the removal of large-bodied species.

a. Tropical habitats.

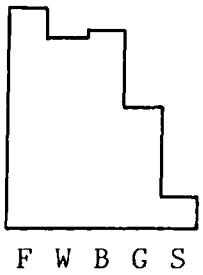
Communities from the four tropical habitat types derived from the analysis in chapter 4 are described here: Forest type I; forest type II; woodland-bushland; and grassland. THI weightings for African mammals from the tropical region are given in appendix 4 and the unbiased patterns for all the communities in the modern comparative sample are shown in appendix 1. THI patterns are shown only at specific level and the habitat types of communities in the modern tropical sample are shown in table 4.11.

Figure 5.1. THI pattern of a Forest type I community.



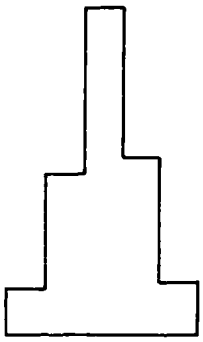

This forest type is distinguished by a very high proportion in the forest column (F) and low values in all other columns. The patterns figured in appendix 1 show that this pattern is consistently found in all forest type I communities, with variation occurring only in the degree of dominance shown by the forest column.

Figure 5.2. THI pattern of a Forest type II community.



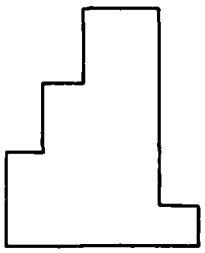

This forest type is distinguished by more or less equal values in the forest (F), woodland (W) and bushland (B) columns. The unbiased THI patterns of forest type II communities figured in appendix 1 show that this pattern is quite variable and appears to be an intermediate between forest type I and woodland-bushland communities.

Figure 5.3. THI pattern of a Woodland-bushland community.




Woodland-bushland communities are distinguished by a high proportion in the bushland column (B), equal but moderate values in the woodland (W) and grassland (G) columns and low values in the forest (F) and semidesert (S) columns. This pattern is apparently consistent among all the woodland-bushland communities in the modern sample (see appendix 1).

Figure 5.4. THI pattern of a Grassland community.




The typical pattern of grassland and floodplain communities shows more or less equal proportions in the bushland (B) and grassland (G) columns, with a moderate value in the woodland column (W) and low proportions in the other two columns (see appendix 1). However, some habitats classified physiognomically as floodplain or grassland have THI patterns more similar to forest type II and woodland-bushland.

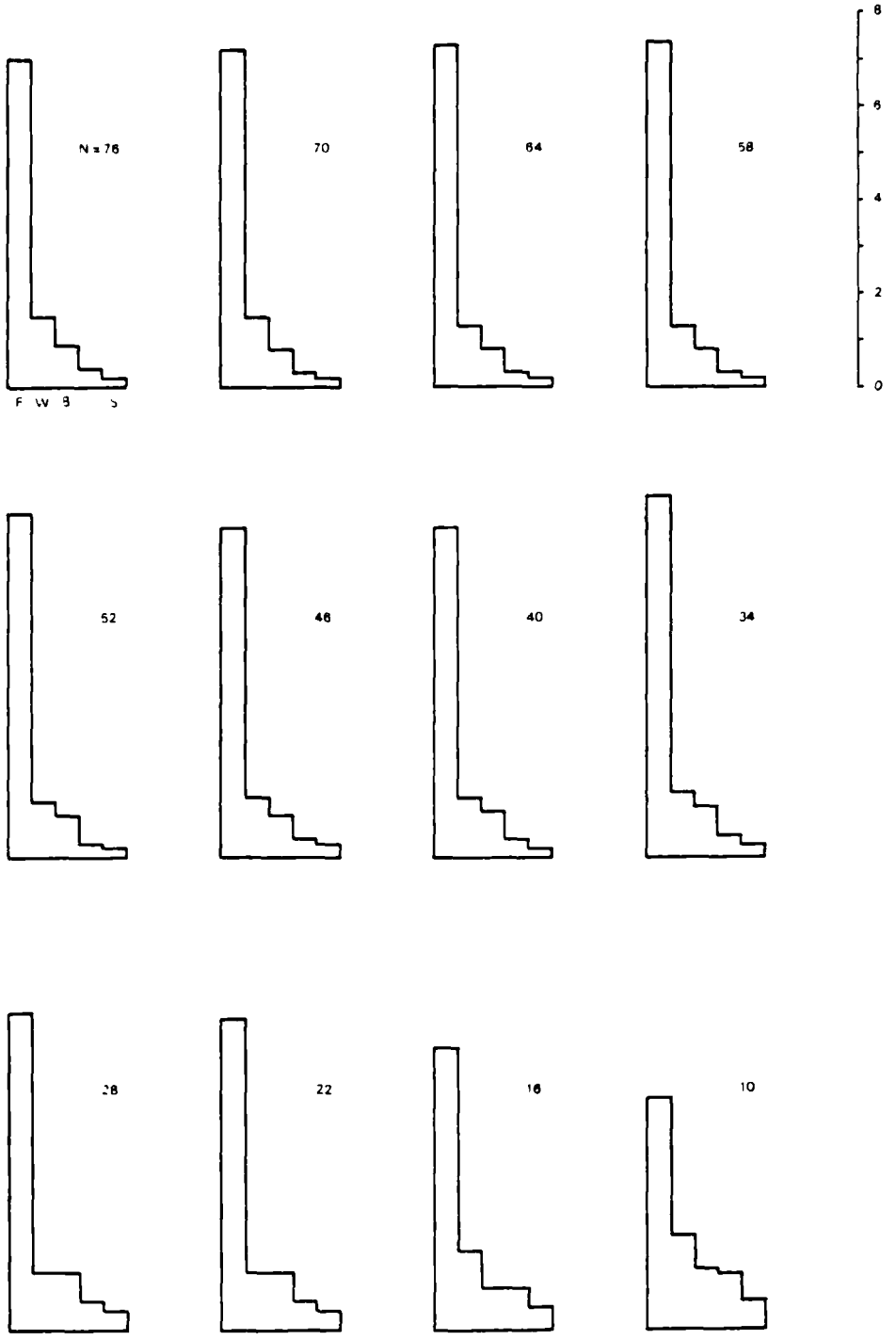
THI simulations: Tropical habitats.

Forest type I: Specific level.

Figure 5.5. Small-bodied species removed.

The features of the unbiased pattern are retained during the simulation. The forest column is strongly dominant throughout although the degree of this dominance diminishes slightly towards the final stages once the species richness has been reduced to less than 20 species.

Figure 5.5.



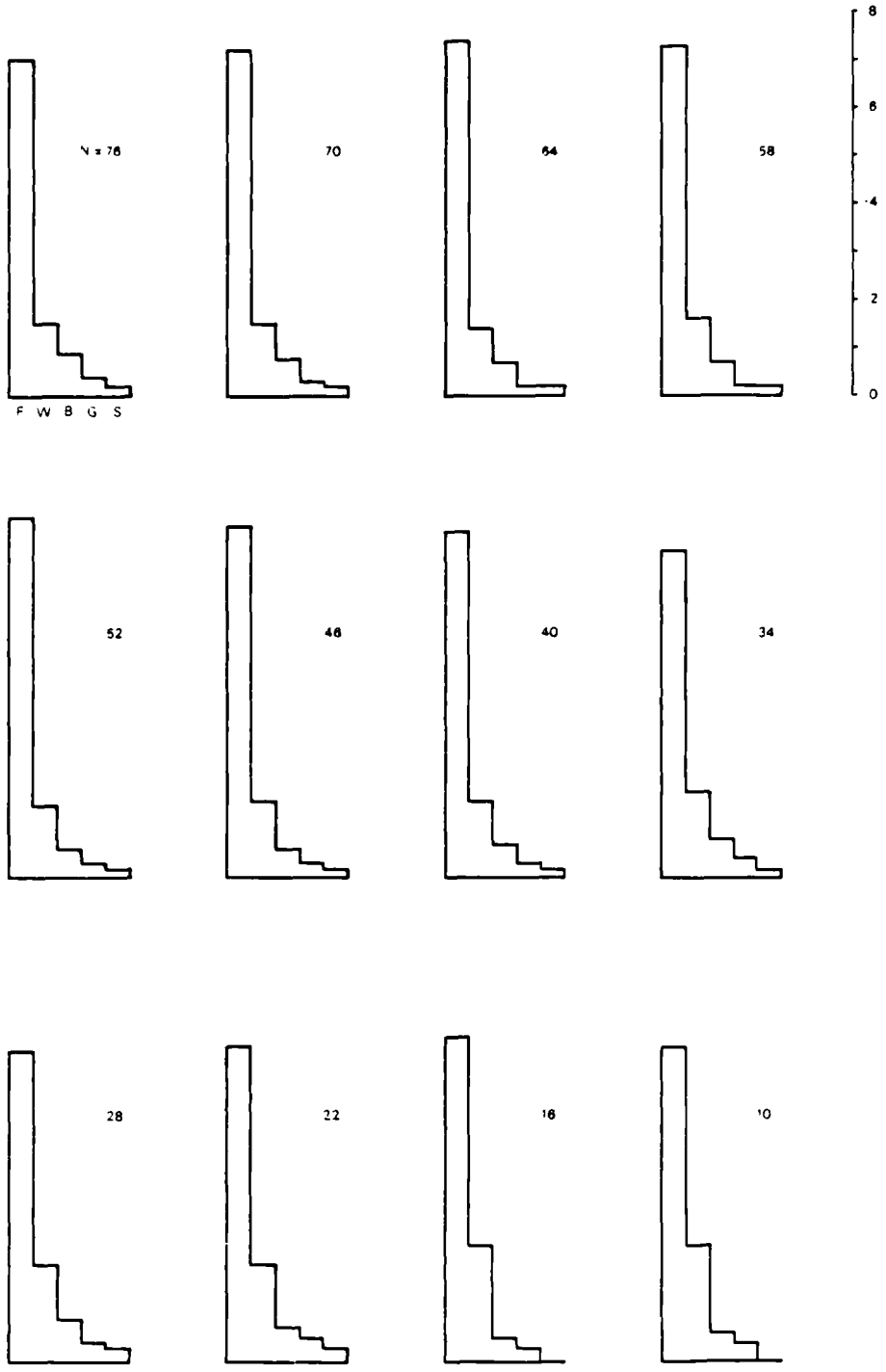
THI simulations: Tropical habitats.

Forest type I: Specific level.

Figure 5.6. Large-bodied species removed.

Once again the essential features of the unbiased pattern are preserved throughout the series. The forest column remains dominant but there are some changes in the importance of the minor columns. Most marked is the gradual increase in the relative importance of the woodland column until it attains a moderate value at the end of the series.

Figure 5.6.



THI simulations: Tropical habitats.

Forest type II: Specific level.

Figure 5.7i. Small-bodied species removed.

The unbiased pattern for this community type shows a slight dominance of the forest column, with the woodland and bushland columns of similar value and the grassland and semidesert columns lower in value. With the exception of the final stage in the series where the woodland and bushland columns are equal and higher in value than the forest and other columns, the basic form of the unbiased pattern is preserved, albeit with some variability of the proportions in the forest, woodland and bushland columns.

Figure 5.7ii. Large-bodied species removed.

This simulation shows somewhat more variability than the preceding one. The general appearance of the unbiased pattern is retained in that the first three columns are more or less equal in value throughout, although the highest value passes between them at various stages. The grassland column grows in importance until it becomes the most important once the species richness has been reduced to a value of 10 species.

Figure 5.7i.

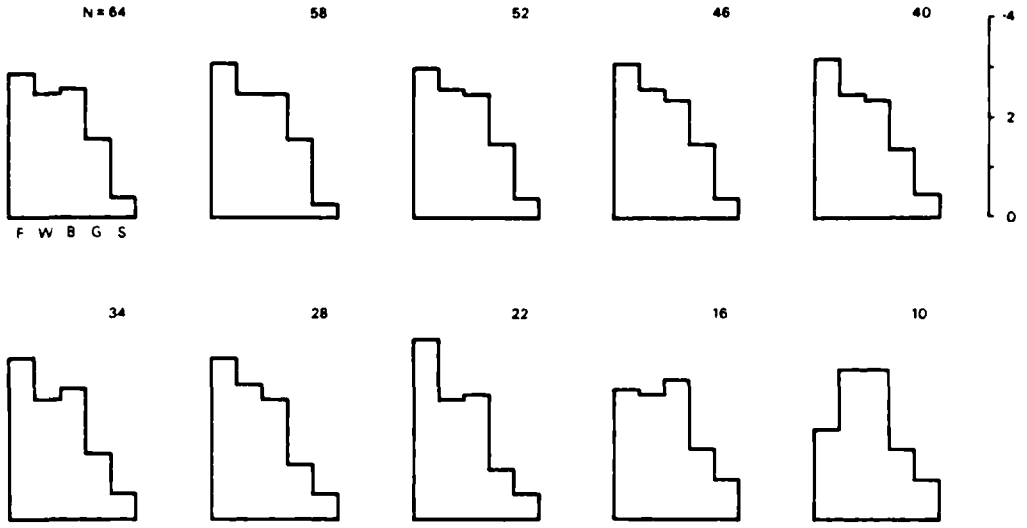
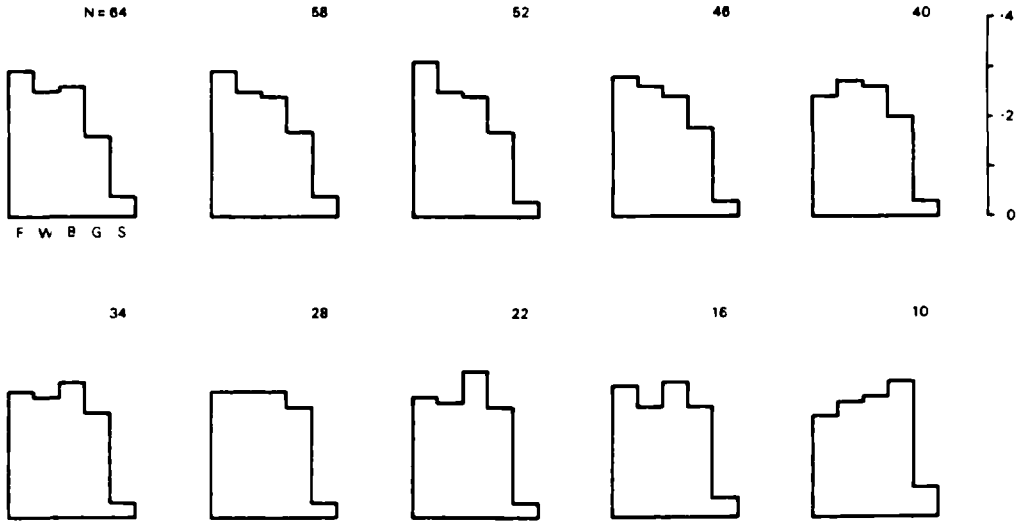



Figure 5.7ii.



THI simulations: Tropical habitats.

Woodland-bushland: Specific level.

Figure 5.8i. Small-bodied species removed.

The essential feature of the unbiased pattern is the dominance of the bushland column. During the removal of small-bodied species there is some variability in the values of the forest, woodland, grassland and semidesert columns, but the bushland column remains the most important throughout.

Figure 5.8ii. Large-bodied species removed.

During the removal of large-bodied species the relative dominance of the bushland column decreases slightly while the relative importance of the forest, woodland and grassland columns gradually increases. In spite of these changes however, the bushland column contains the highest proportion during the whole simulation and a recognisable woodland-bushland pattern is preserved.

Figure 5.8i.

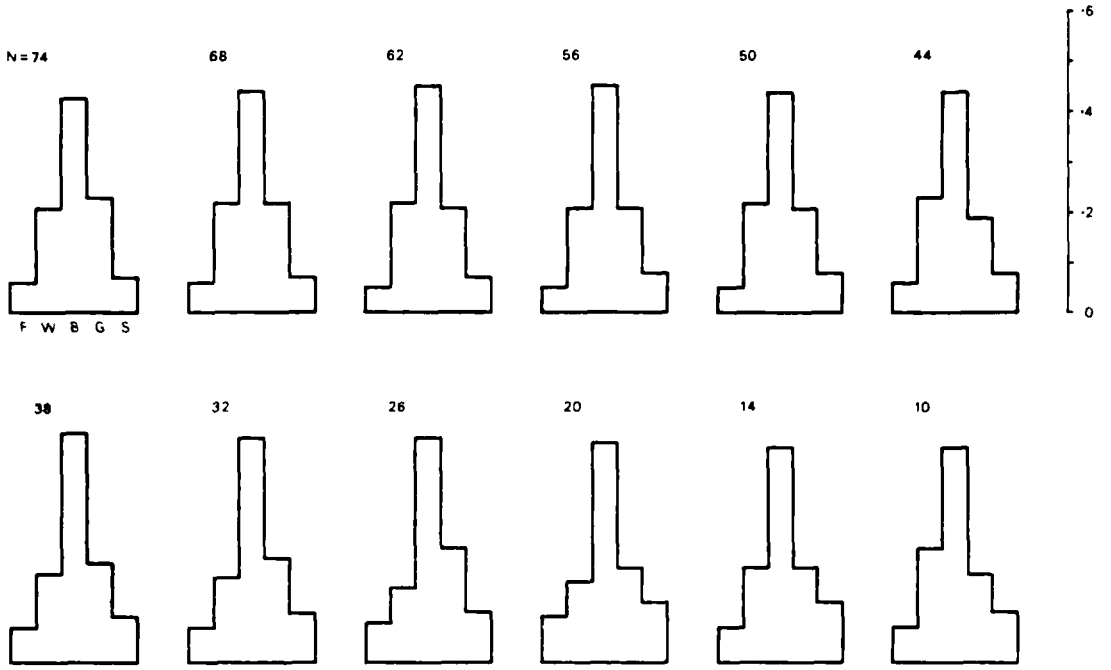
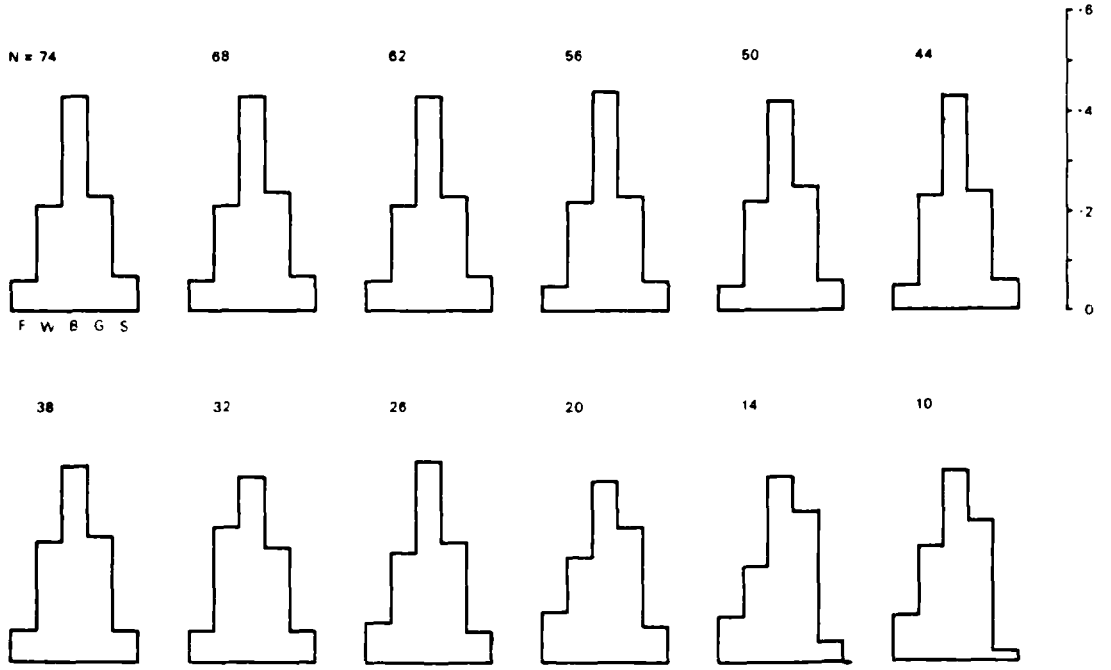



Figure 5.8ii.



THI simulations: Tropical habitats.

Grassland (+ floodplain): Specific level.

Figure 5.9i. Small-bodied species removed.

The unbiased pattern of this community type is characterised by the bushland and grassland columns having the greatest values, while the woodland column contains only a moderate proportion. During the removal of small bodied species the pattern tends first towards the type of profile shown by woodland-bushland communities (see figures 5.3, 5.8i and 5.8ii), where the bushland column dominates. This column then becomes decreasingly important and the grassland column increases in proportion until by the end of the simulation it is the most important.

Figure 5.9ii. Large-bodied species removed.

Once again, there is initially a brief tendency towards the woodland-bushland form of pattern. The column representing grassland habitats then assumes a gradually increasing importance, until by the end of the simulation it dominates all the other columns.

Figure 5.9i.

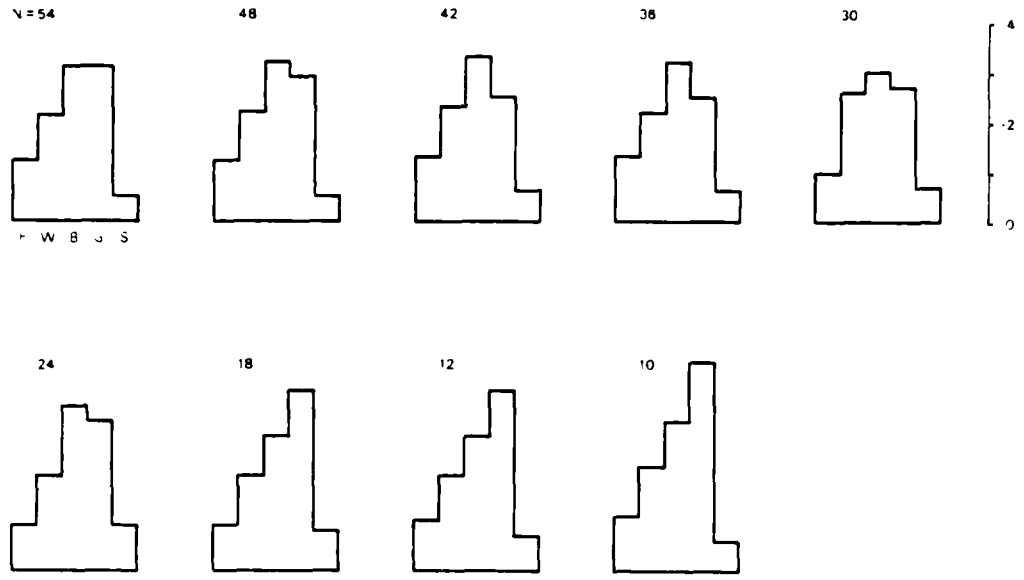
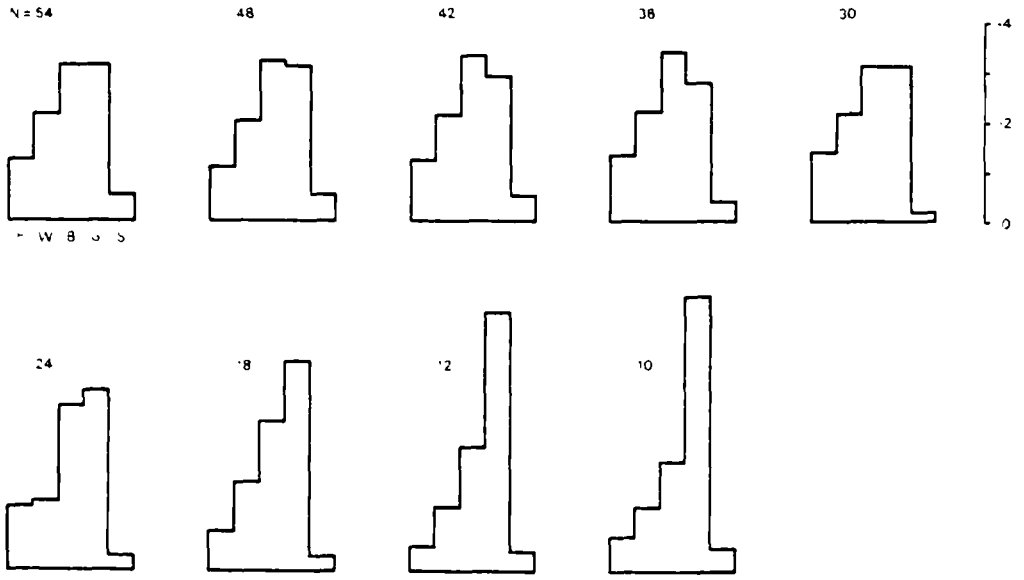


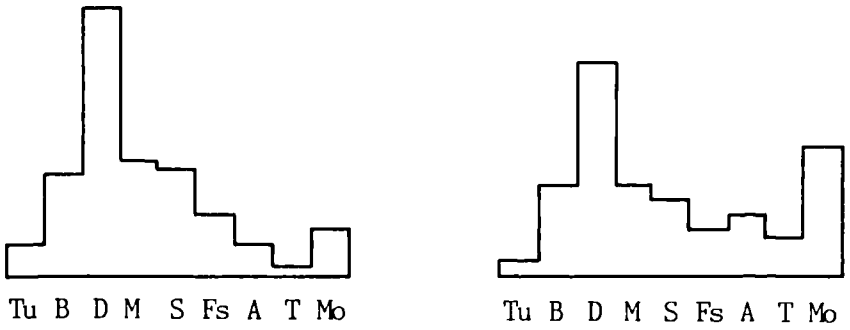

Figure 5.9ii.



b. Temperate habitats.

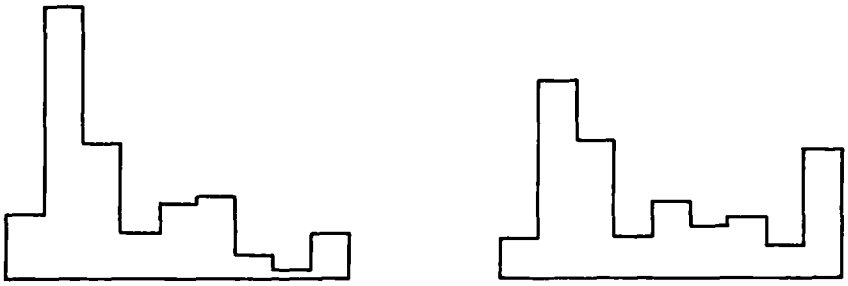
The unbiased specific and generic level THI patterns for communities from six temperate habitat types are described here. Only five of these are used in the simulations since the sixth (semidesert) has only 10 species initially and is thus already at the *de minimis* limit for the simulation series. THI weightings for Palaearctic species are given in appendix 3, the unbiased specific level THI patterns for all the communities in the modern Palaearctic sample are shown in appendix 2, and the habitats of each of these communities are listed in table 4.20.

Figure 5.10. THI pattern of a deciduous forest community.




Deciduous forest communities have THI patterns characterised by a strong dominance of the deciduous forest column (D), accompanied by lower but approximately equal values in the boreal (B), mediterranean (M) and steppe (S) columns. The tundra column (Tu) has a low value and the montane column (Mo) has a moderate value only in the generic level pattern. It should be noted that a moderate value in the montane column is a character commonly found in generic level patterns.

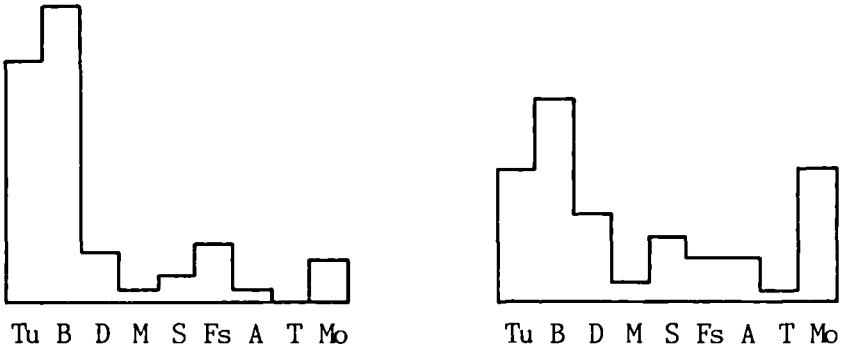
Figure 5.11. THI pattern of a boreal forest community.




Species Genera

The distinctive character of boreal forest patterns is the high proportion in the boreal forest column (B) and the moderate value in the deciduous forest column (D). The montane column (Mo) also attains a moderate value in the generic level pattern.

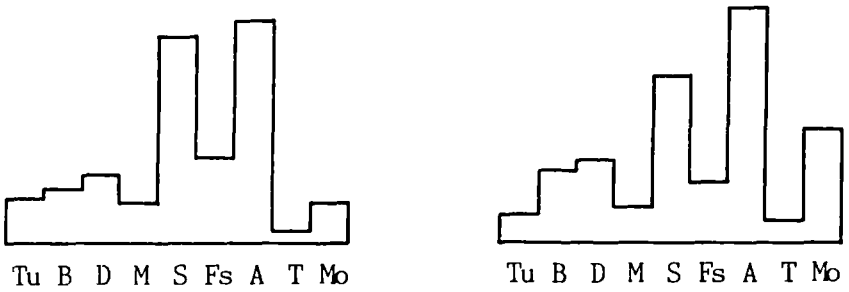
Figure 5.12. THI pattern of a tundra community.




Species Genera

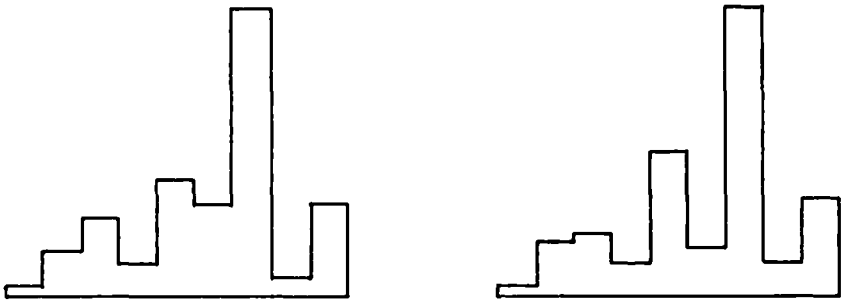
The THI patterns of 8 ecological and 6 geographical communities from tundra habitats are shown in figure 4.3. Tundra community THI patterns are distinguished primarily by a high value in the tundra column (Tu). In some cases, as in the figures illustrated here, the proportion in the tundra column is exceeded by that in the boreal forest column (B). The other columns of the profile all have low values although the montane column (Mo) reaches a moderate value in the generic level pattern.

Figure 5.13. THI pattern of a steppe community.



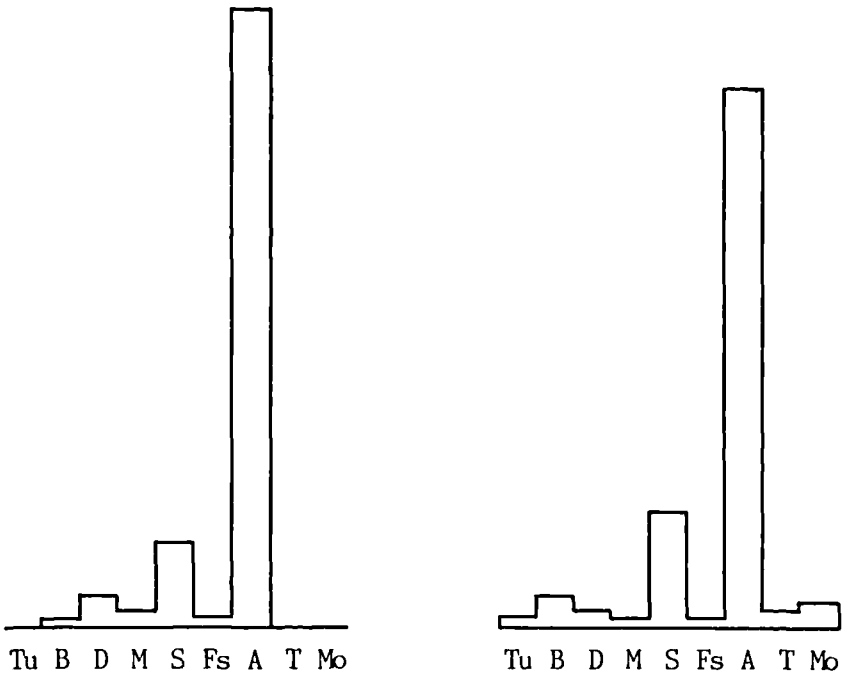

The steppe pattern is distinguished by high values in two columns, the steppe (S) and arid steppe /semidesert (A) columns. These are approximately equal in the specific level pattern, but the arid steppe/semidesert column is the greater in the generic level pattern. The forest-steppe column (Fs) has a moderate value in the specific level pattern and the montane column (Mo) attains a moderate proportion in the generic level pattern.

Figure 5.14. THI pattern of a semidesert community.




The unbiased semidesert pattern resembles that for steppe communities in that it is distinguished by high values in the columns representing steppe (S) and arid steppe/semidesert (A). This latter column has the highest proportion at both specific and generic levels, while the forest-steppe column (Fs) attains a moderate proportion in the specific level pattern.

Figure 5.15. THI pattern of a desert community.




Desert communities are characterised by a pattern in which the column representing arid habitats (A) have extremely high values in both specific and generic level patterns. The steppe column (S) reaches a moderate value in the generic level pattern.

THI simulations: Temperate habitats.

Deciduous forest: Specific level.

Figure 5.16i. Small-bodied species removed.

The initial unbiased pattern is preserved throughout most of this simulation. The deciduous forest column retains its high value although the pattern as a whole becomes less distinctive towards the end of the simulation where the value of the mediterranean column increases and the values of the steppe and boreal forest columns decrease.

Figure 5.16ii. Large-bodied species removed.

With the removal of large-bodied species the pattern retains the characteristic appearance of the unbiased pattern. Indeed, the importance of the deciduous forest column actually increases towards the end of the series.

Figure 5.16i.

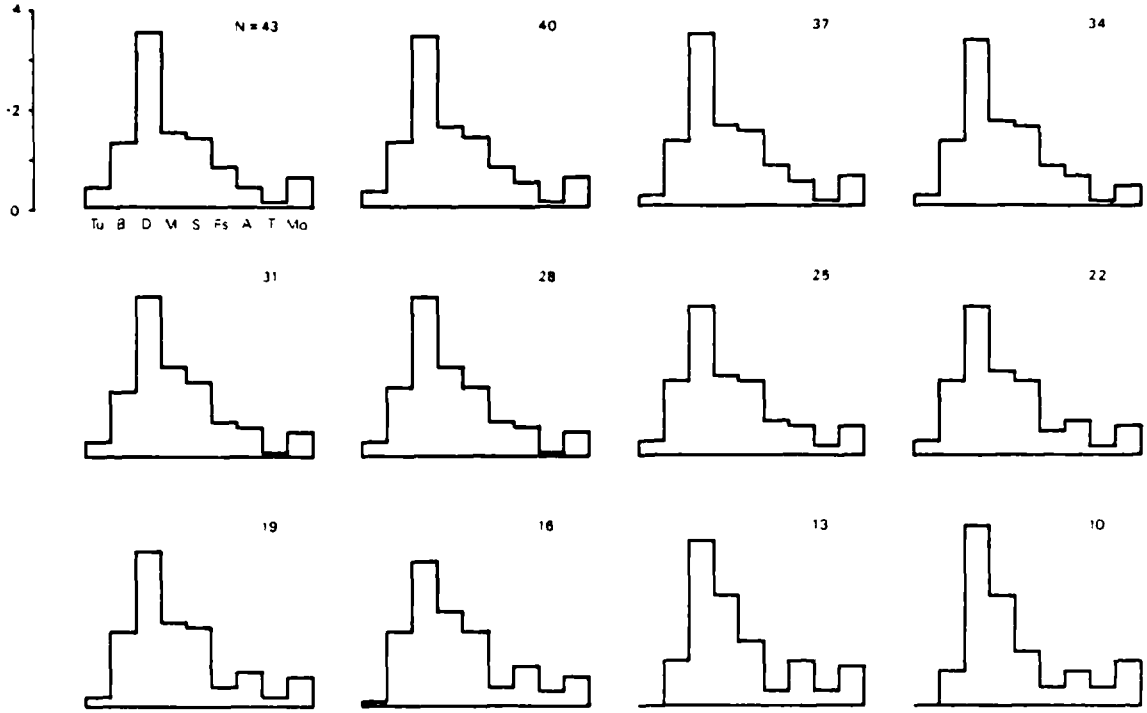
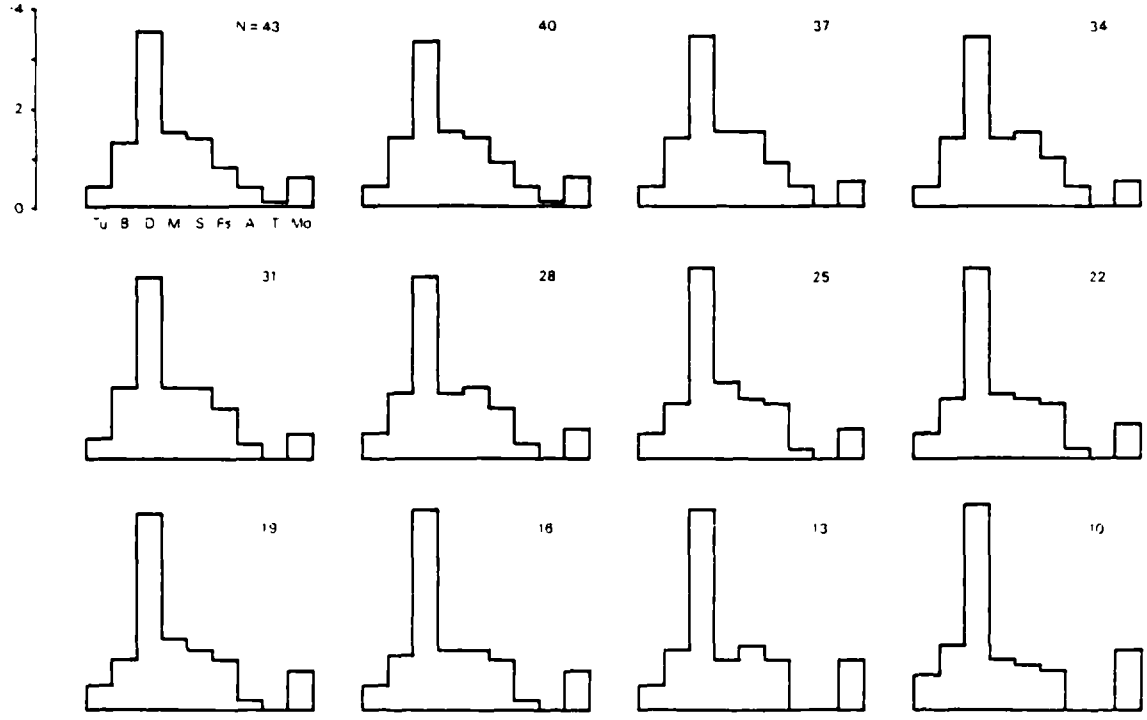



Figure 5.16ii.



THI simulations: Temperate habitats.

Deciduous forest: Generic level.

Figure 5.17i. Small-bodied species removed.

The importance of the deciduous forest column is maintained throughout the series. The values of the mediterranean and tropical columns increase gradually during the simulation, while that of the montane column is reduced slightly. However, in spite of these changes, a recognisable deciduous forest profile is still apparent even at the end of the simulation.

Figure 5.17ii. Large-bodied species removed.

The unbiased pattern is preserved with very little alteration apart from the fact that the montane column shows a considerable increase in importance. By the end of the simulation this column has the highest value of all, but the deciduous forest pattern is still clearly recognisable in the rest of the pattern.

Figure 5.17i.

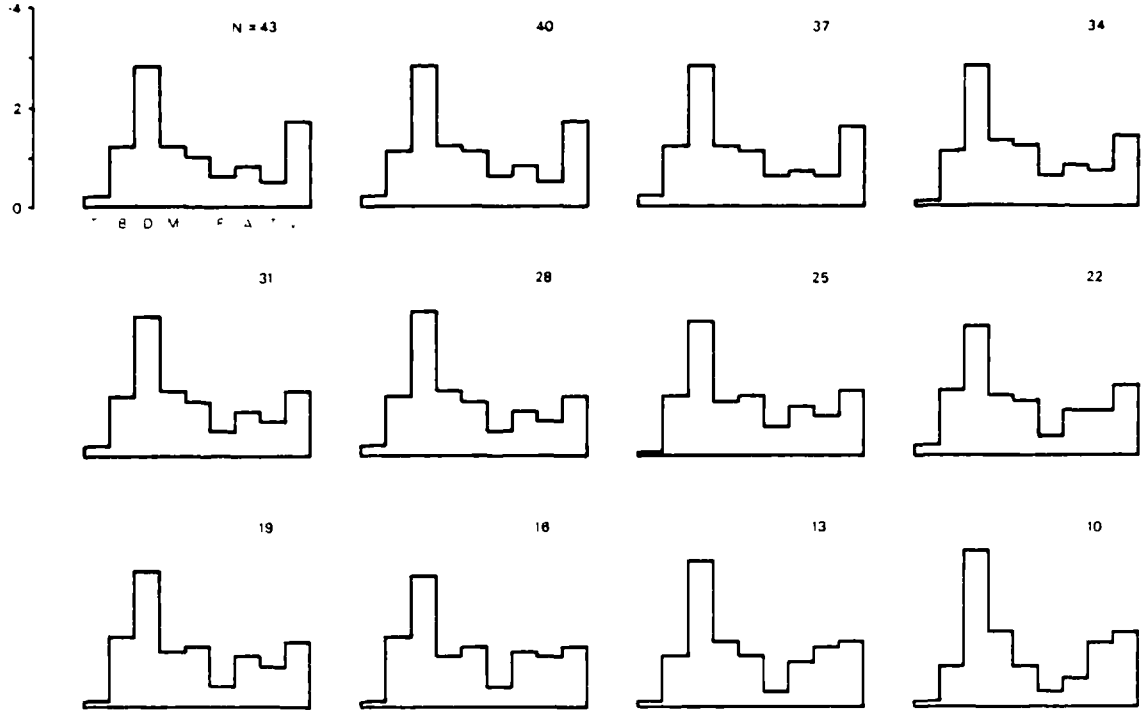
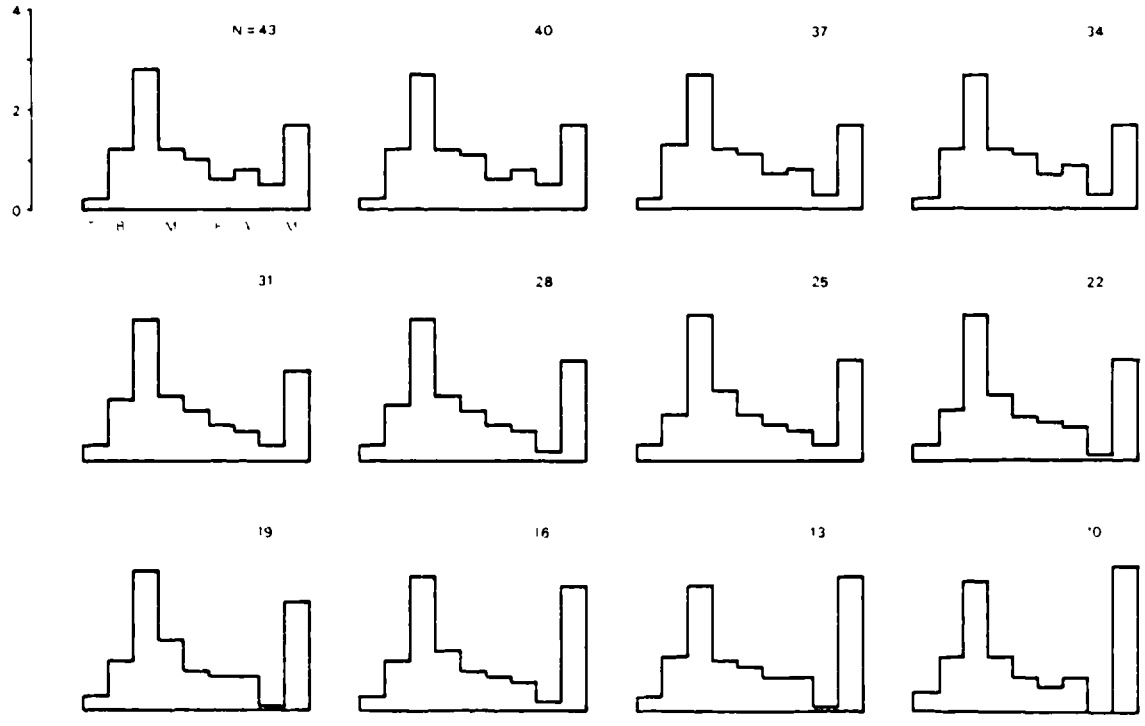



Figure 5.17ii.



THI simulations: Temperate habitats.

Boreal forest: Specific level.

Figure 5.18i. Small-bodied species removed.

The unbiased pattern is preserved during this simulation with relatively little variation. There is a gradual trend involving an increase in the dominance of the boreal forest column, while the relative importance of all the other columns is reduced.

Figure 5.18ii. Large-bodied species removed.

Once again, the unbiased pattern is preserved through the whole of the simulation. In the final stages the importance of the boreal forest column increases, accompanied by an increase in the relative importance of the tundra and deciduous forest columns.

Figure 5.18i.

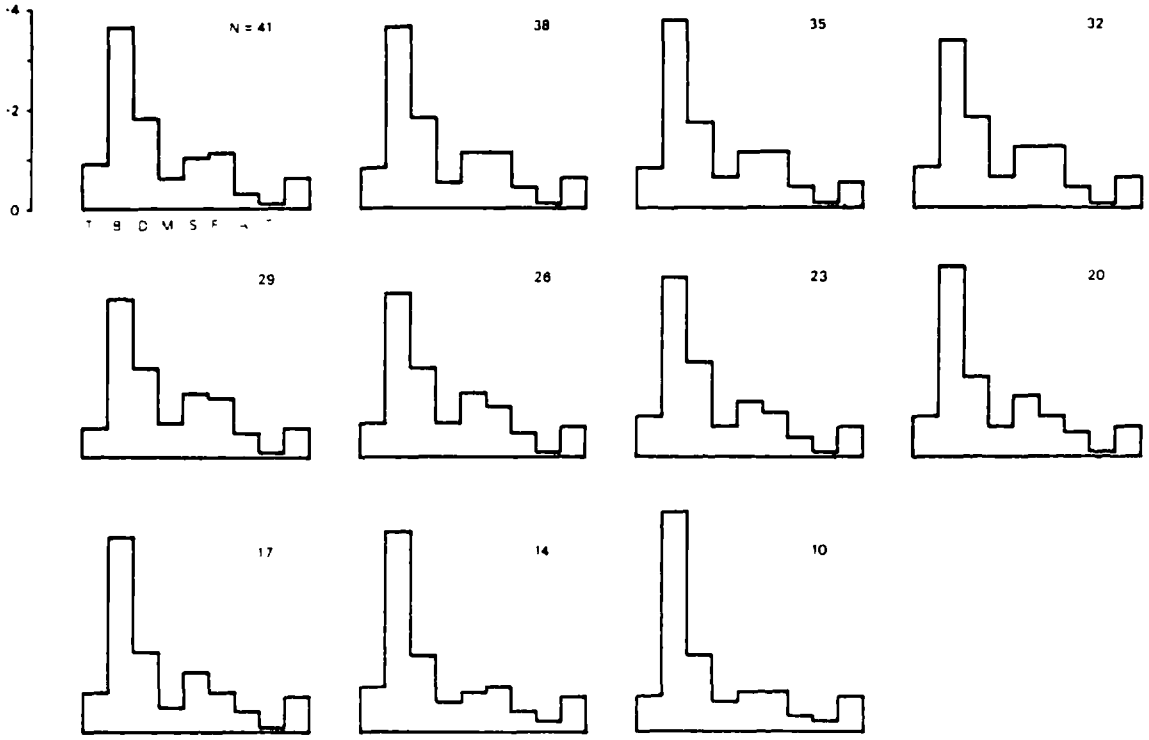
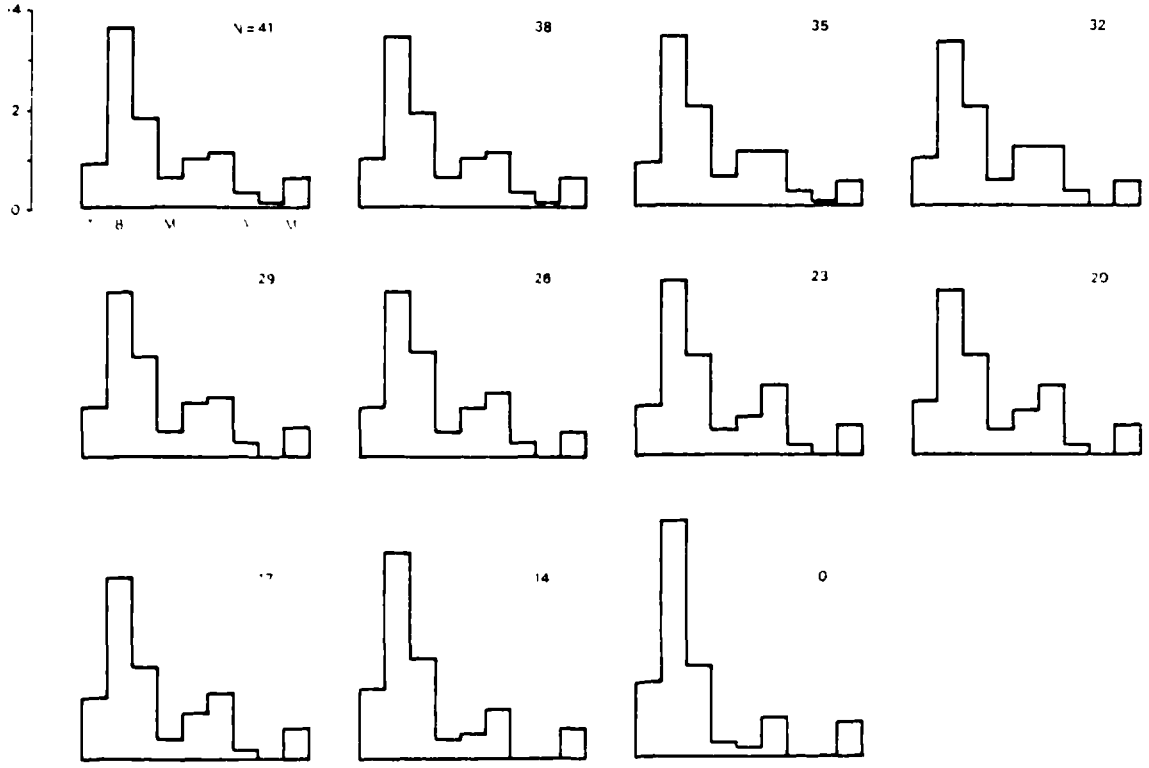



Figure 5.18ii.



THI simulations: Temperate habitats.

Boreal forest: Generic level.

Figure 5.19i. Small-bodied species removed.

The importance of the boreal forest column gradually increases during the simulation while at the same time the relative importance of both the deciduous forest and montane components decreases. The result is a pattern strongly dominated by the boreal forest column.

Figure 5.19ii. Large-bodied species removed.

The initial change upon the removal of large-bodied species is an increase in the importance of the deciduous forest and montane columns relative to that of the boreal forest column. The effect is to give all three columns approximately equal values. Towards the end of the series the boreal forest column once again becomes higher in value than the deciduous forest column and a pattern similar to that of the unbiased community is restored. However, the value of the montane component is higher than in the unbiased pattern and is similar to the value of the boreal forest column during most of the simulation.

Figure 5.19i.

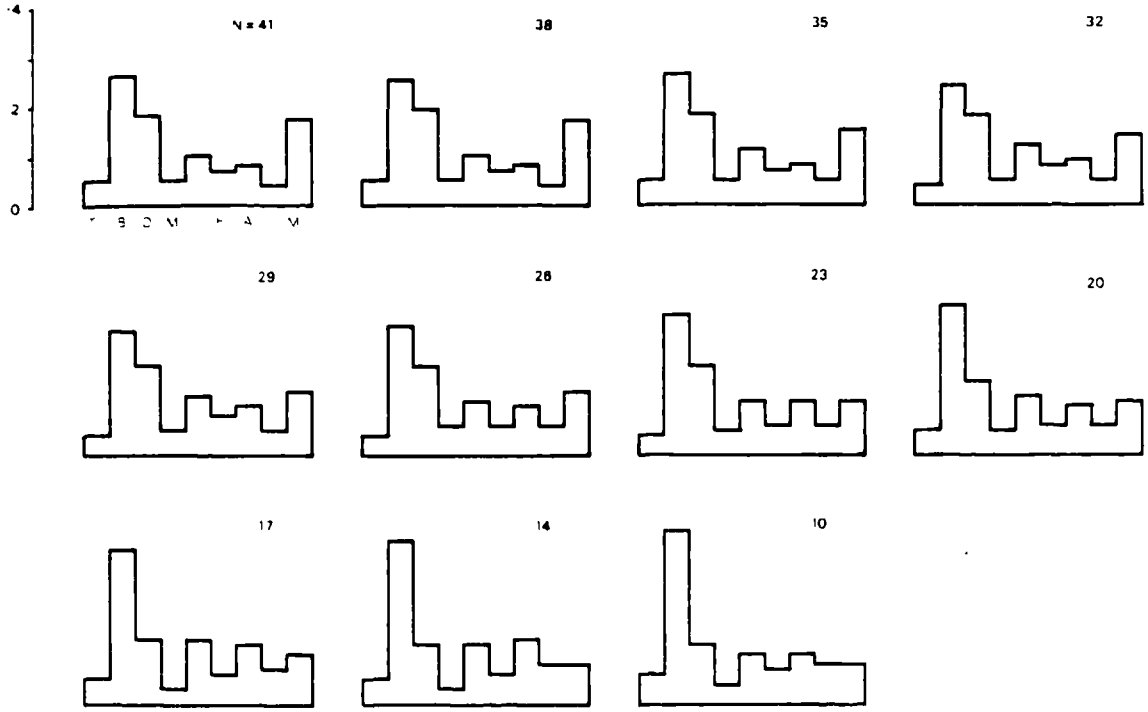
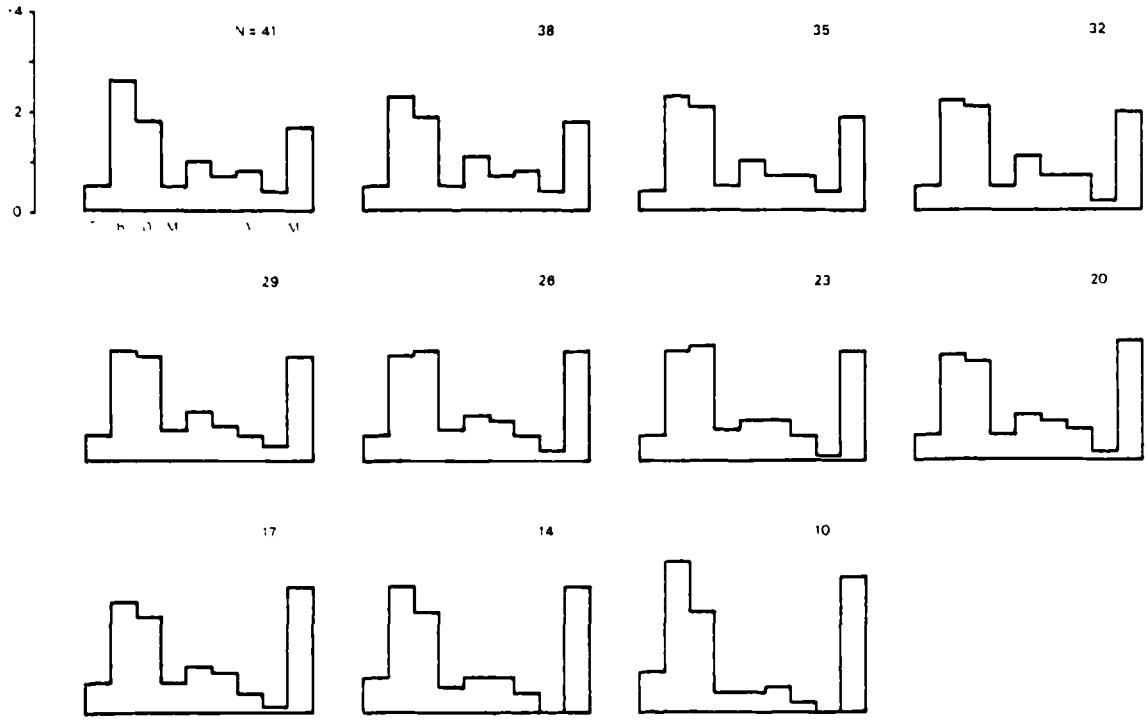



Figure 5.19ii.



THI simulations: Temperate habitats.

Tundra: Specific level.

Figure 5.20i. Small-bodied species removed.

Tundra patterns are distinguished primarily by high values in the tundra and boreal forest columns. This characteristic is preserved throughout this simulation with relatively little variation apart from the fact that the values in these two columns becomes equal in the middle part of the series.

Figure 5.20ii. Large-bodied species removed.

The unbiased pattern is preserved with practically no alteration during the first part of the sequence. Towards the final stages the relative importance of the boreal forest column increases slightly, but the tundra column still retains a high value.

Figure 5.20i.

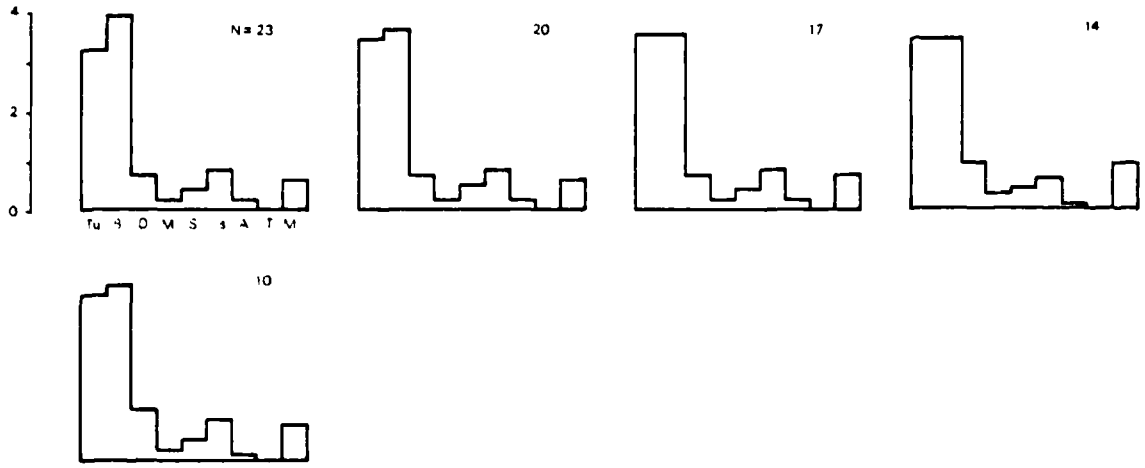
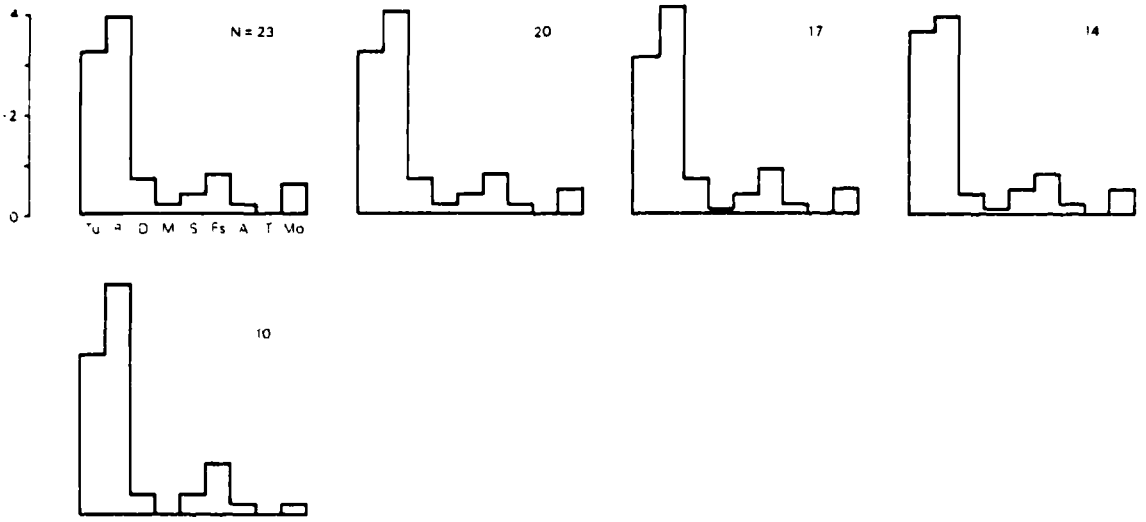



Figure 5.20ii.



THI simulations: Temperate habitats.

Tundra: Generic level.

Figure 5.21i. Small-bodied species removed

The unbiased pattern is retained almost completely intact throughout the simulation. The relative importance of both the tundra and boreal forest columns increases gradually. The values in most of the other columns are reduced and the decrease is most noticeable in the column representing montane habitats.

Figure 5.21ii. Large-bodied species removed.

The unbiased pattern is relatively stable during this simulation, although in the middle part of the series a pattern emerges which is similar to those given by boreal forest communities (see figures 5.18 and 5.19). The tundra pattern is distinguished, however, by the value of the tundra column, which is higher than that found in comparable boreal forest patterns. The final pattern resembles that of the unbiased community quite closely although the relative importance of the montane column column has increased slightly.

Figure 5.21i.

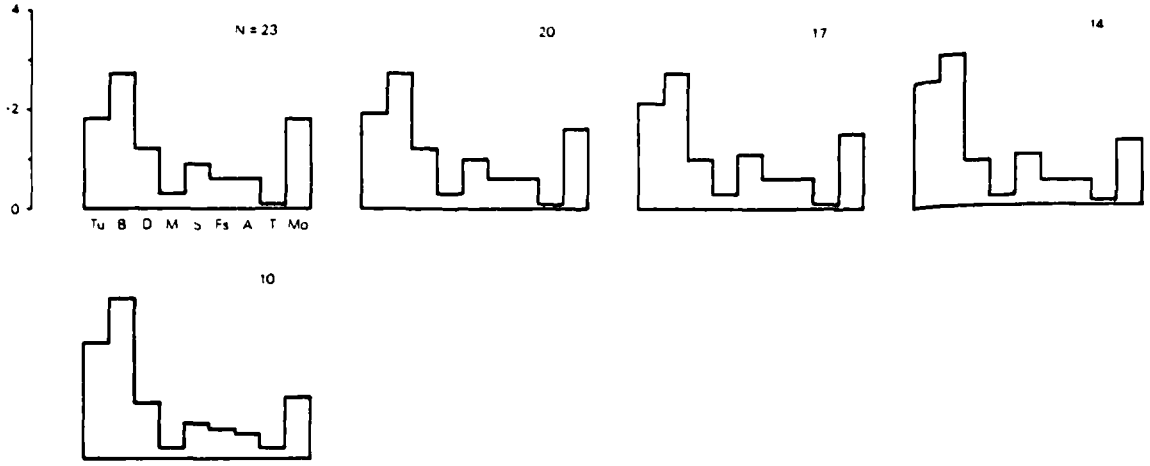
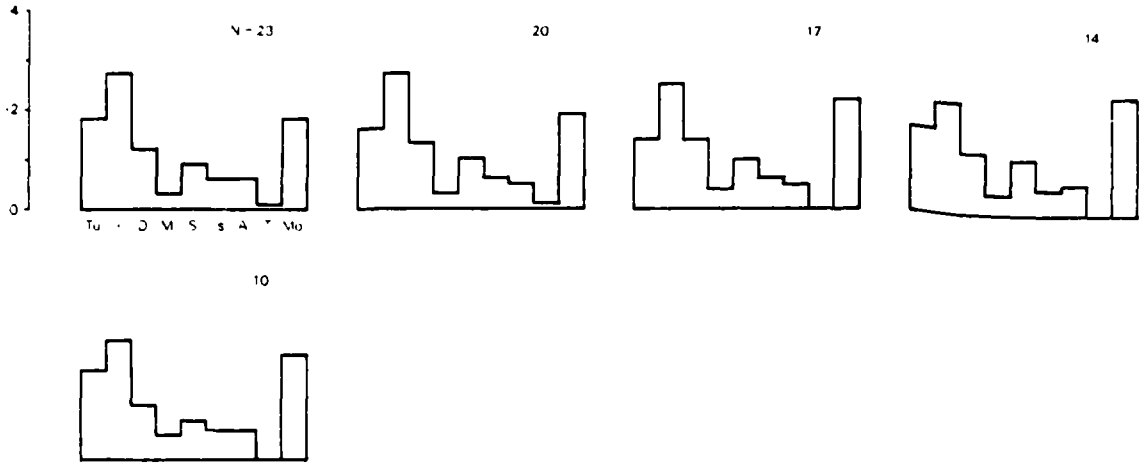



Figure 5.21ii.



THI simulations: Temperate habitats.

Steppe: Specific level.

Figure 5.22i. Small-bodied species removed.

The unbiased pattern is preserved relatively intact although there are gradual changes which by the end of the sequence result in the relative importance of tundra, boreal forest and deciduous forest columns having increased, while the relative importance of the columns representing steppe and arid habitats is reduced slightly.

Figure 5.22ii. Large-bodied species removed.

The initial pattern remains virtually unchanged. Towards the end of the simulation, the values in the first three columns increase slightly at the expense of the steppe and arid habitats columns.

Figure 5.22i.

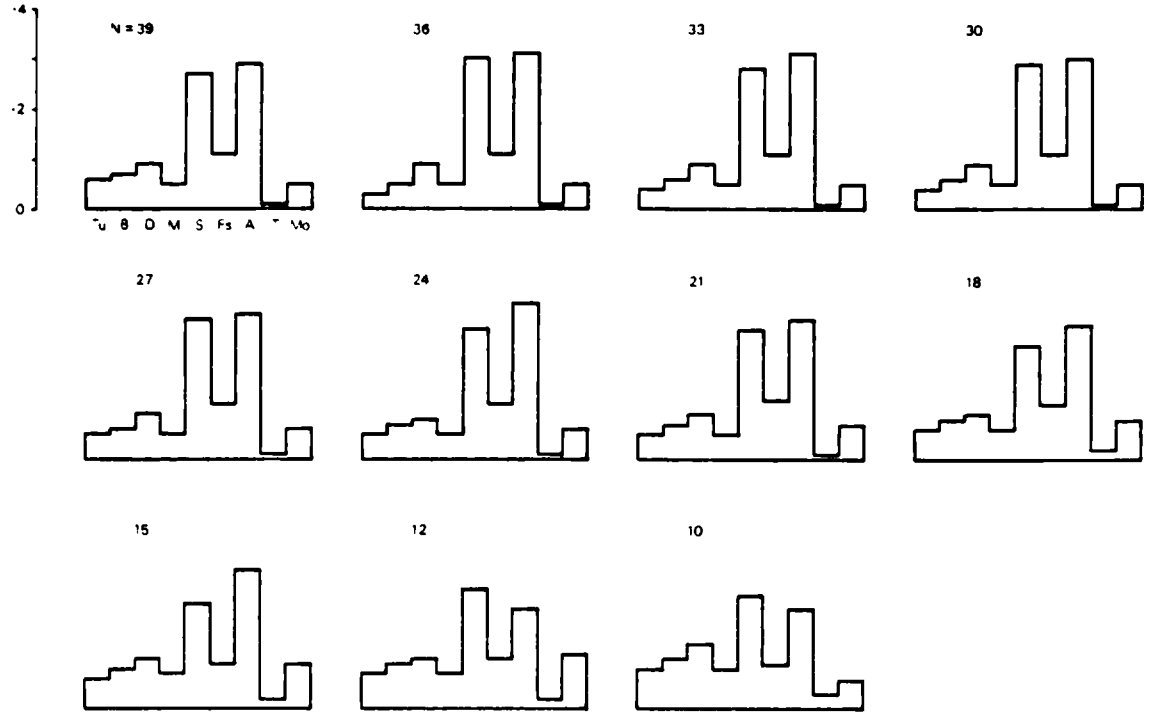
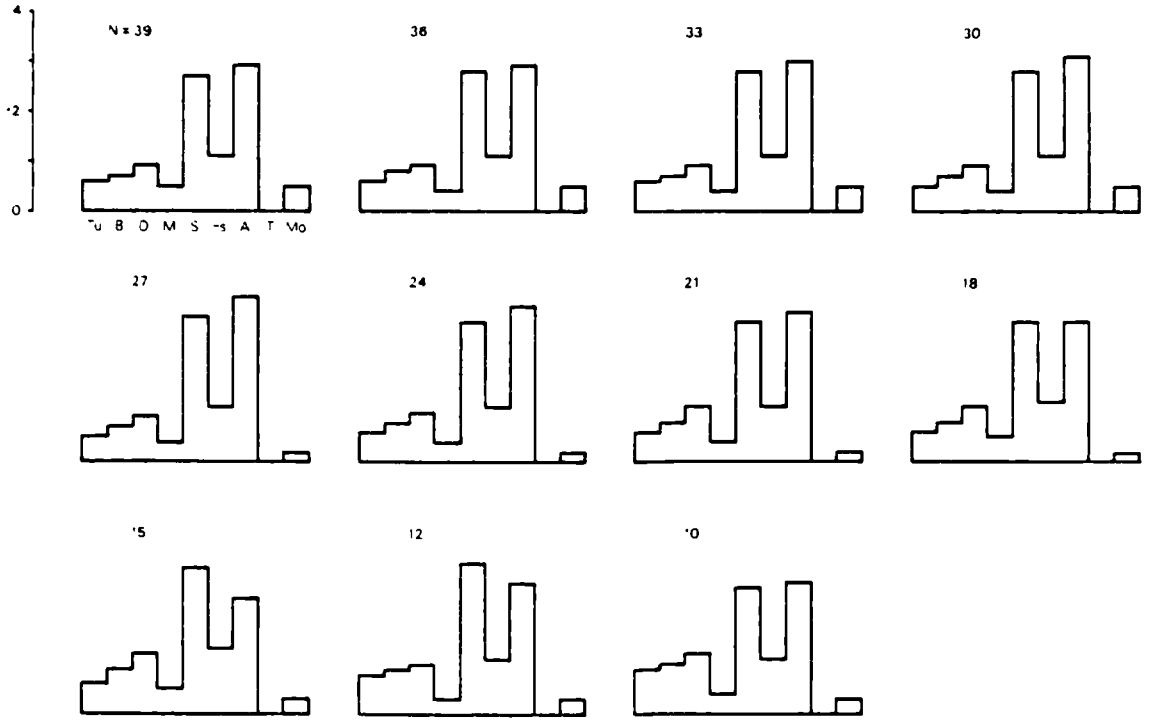



Figure 5.22ii.



THI simulations: Temperate habitats.

Steppe: Generic level.

Figure 5.23i. Small-bodied species removed.

The initial pattern is stable through the whole of the series of patterns illustrated and a characteristic steppe pattern is preserved. The relative importance of the steppe and arid habitats columns decreases slightly towards the end of the series but this does not affect the overall distinctiveness of the pattern.

Figure 5.23ii. Large-bodied species removed.

Once again a remarkable stability is displayed and despite some increase in the relative importance of the boreal forest, deciduous forest and montane columns, the pattern remaining at the end of the sequence is still clearly attributable to a steppe community.

Figure 5.23i.

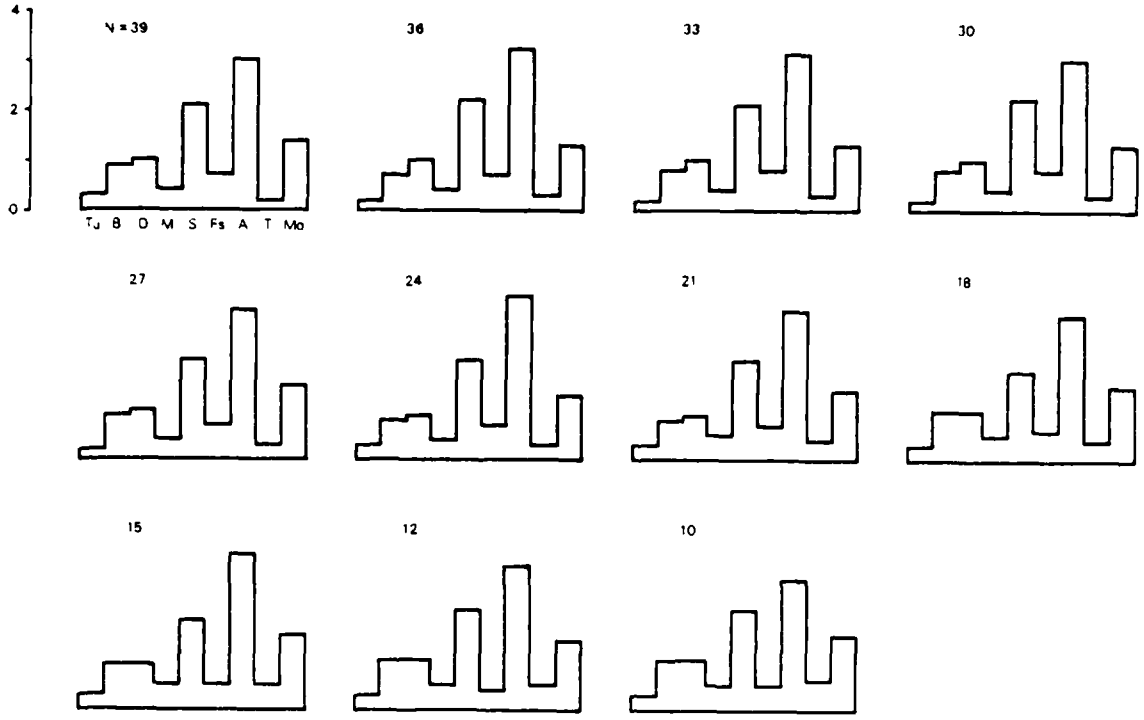
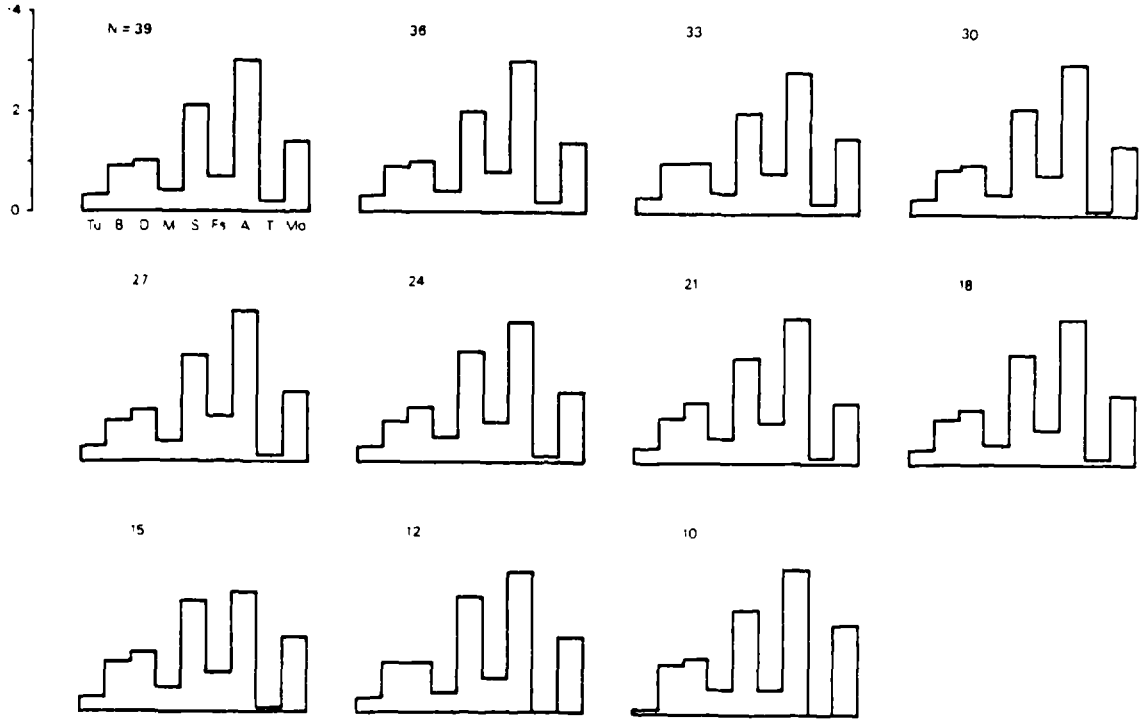



Figure 5.23ii.



THI simulations: Temperate habitats.

Semidesert: Specific level.

Figure 5.24i. Small-bodied species removed.

The initial pattern undergoes considerable alteration during this sequence even after the removal of only 9 to 12 species. The unbiased pattern is dominated by the column representing arid habitats (arid steppe and semidesert), but this dominance gradually decreases as the deciduous forest, steppe and montane columns increase in value. By the final stages the relative importance of these columns equals or exceeds that of the arid steppe/semidesert column.

Figure 5.24ii. Large-bodied species removed.

With the removal of large-bodied species the main features of the unbiased pattern become more exaggerated. The dominance of the column representing arid habitats increases throughout and there is a slight increase in the relative importance of the steppe and forest-steppe columns. In the final stages this pattern resembles that of desert communities, although in no cases do desert patterns show such high values of the steppe and forest-steppe components (see figure 5.15).

Figure 5.24i.

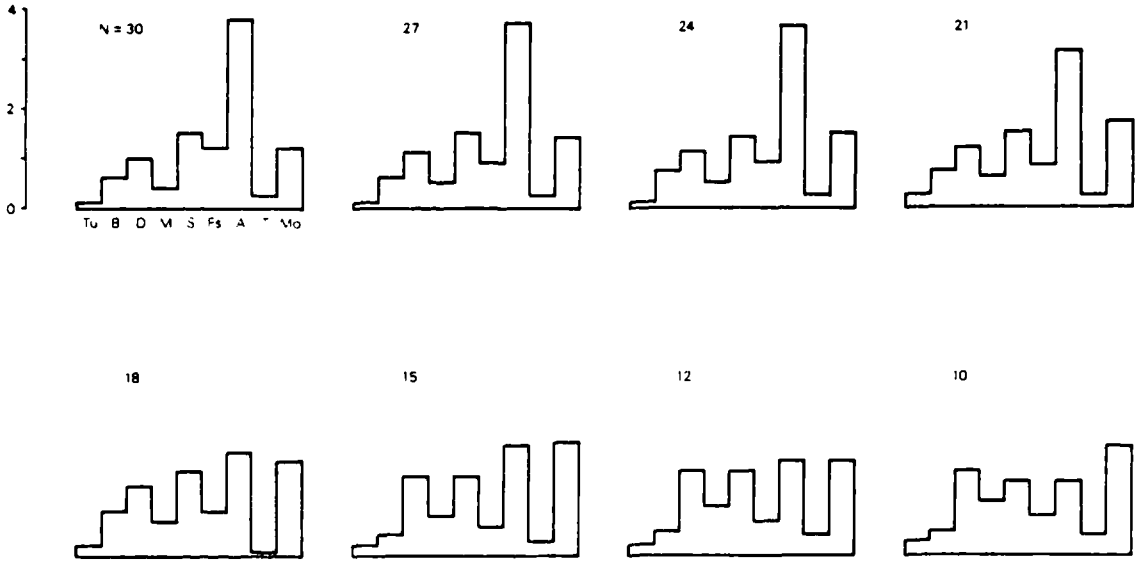
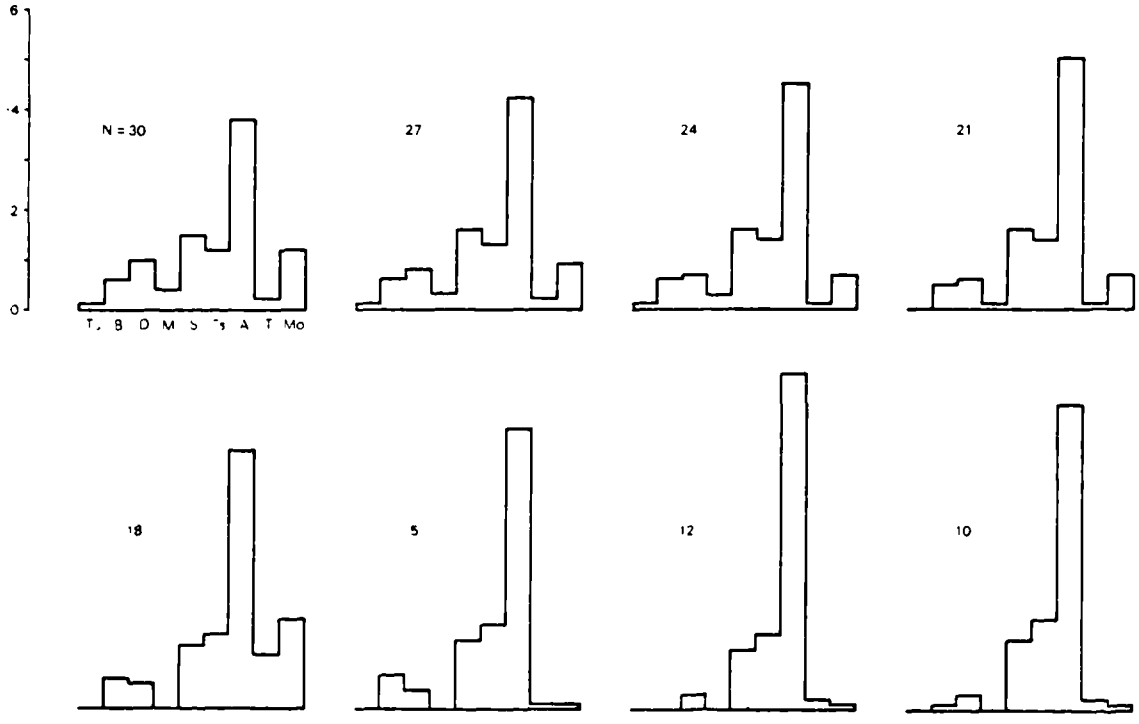



Figure 5.24ii.



THI simulations: Temperate habitats.

Semidesert: Generic level.

Figure 5.25i. Small-bodied species removed.

During the first half of the simulation series the initial pattern is retained with little change. As the simulation progresses, the relative importance of the column representing arid habitats decreases, while the values of the deciduous forest and montane columns increase. There is also some decrease in the value of the steppe component.

Figure 5.25ii. Large-bodied species removed.

The removal of large-bodied species results in the initial pattern becoming more marked as the relative importance of the steppe, forest-steppe and arid habitats columns all increase, while the values in all other columns decrease.

Figure 5.25i.

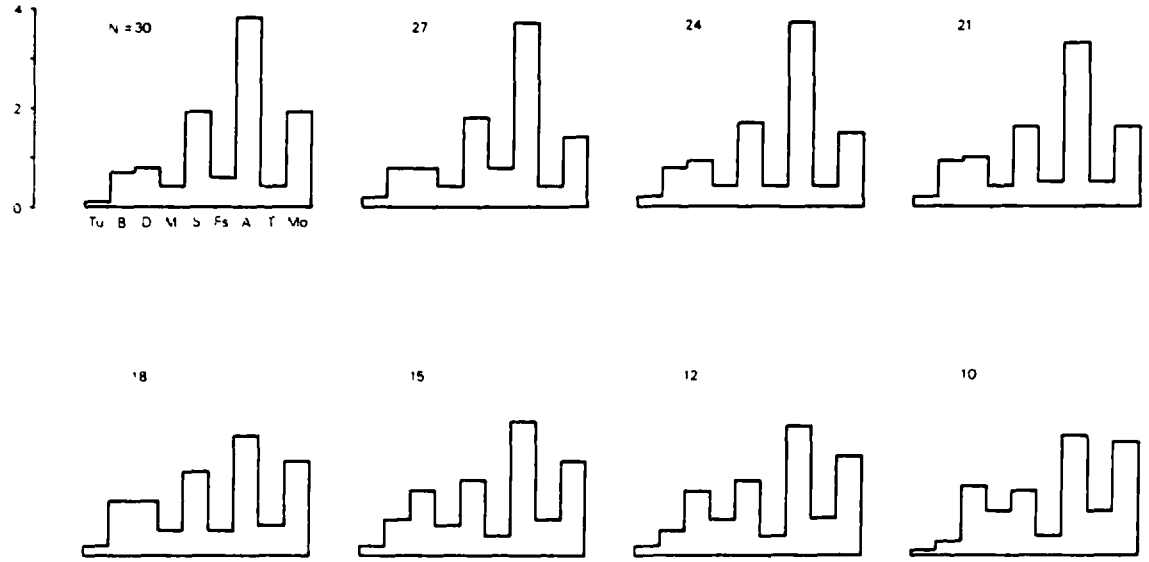
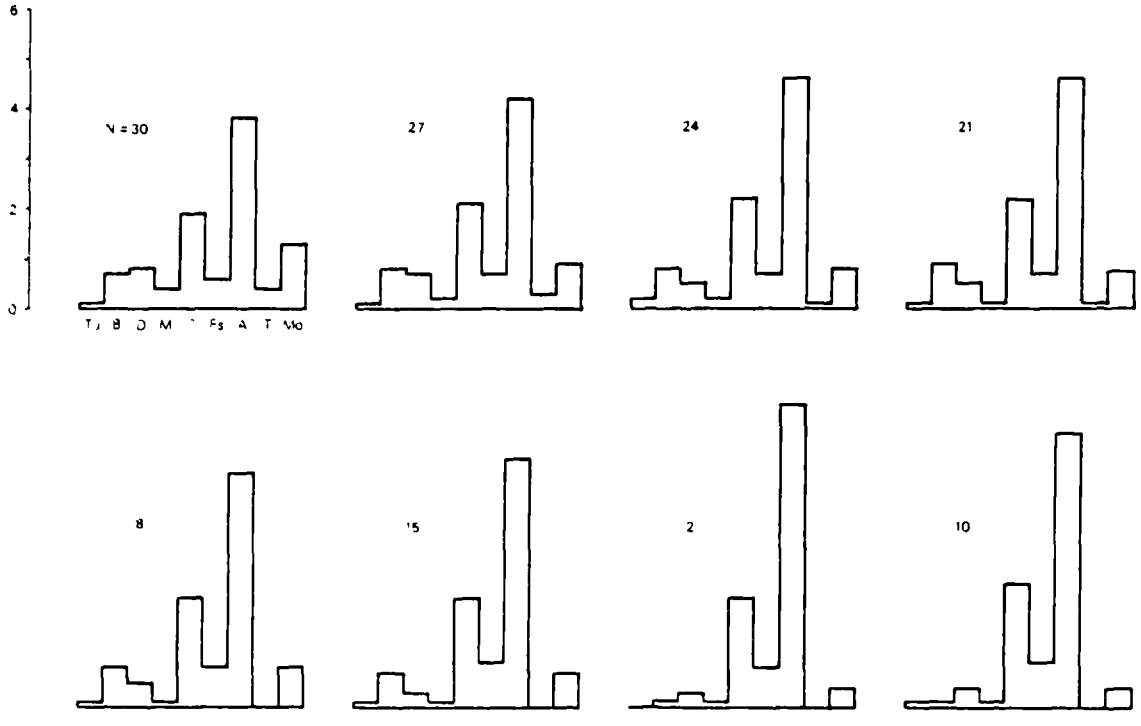



Figure 5.25ii.



c. Conclusions.

The most important and striking point to come out of the simulations described above is that taxonomic habitat index patterns are relatively insensitive to the loss of species from natural communities. With one or two exceptions, the essential characteristics of the unbiased THI patterns for communities from each habitat type are preserved with little alteration through simulation series involving the removal of up to 60 species. This apparently holds true at both specific and generic levels and it seems likely that the same would be found for fossil faunas. The patterns for fossil faunas are usually derived from a mixture of weightings at specific, generic and other levels and it has to be taken into account that THI weightings tend to be more equitable across the habitat range at the generic level than at the specific level (see appendices 3 and 4). This has the consequence that patterns calculated at the generic level tend to be less distinctive.

It was shown in chapter 4 that the THI pattern is independent of whether the community is ecological or geographical. This observation, combined with the fact that the pattern is also independent of community size or the degree of species loss during fossilization, means that THI patterns are extremely useful for the

interpretation of fossil faunas, many of which have in practice suffered taphonomic biases. Furthermore, since detailed information about the nature or extent of species loss is not required, THI patterns can be drawn up independently of taphonomic analyses. All these factors make this a method that is ideally suited to use in the field.

3. Residual Diversity simulations.

Changes in residual diversity patterns were also recorded during the simulations described above. Each modern habitat has a distinctive residual diversity pattern in the unbiased state (see figures 5.26 to 5.29, 5.38 to 5.42 and appendices 1 and 2). These patterns alter gradually as species are lost from a community, but as pointed out in chapter 3, some of the effects of species loss are predictable and can be illustrated by simulations: The value of the distance De, which reflects the effect of those classes in which the base community has excess species, can only be reduced as this excess is reduced through the loss of species from those classes. The proportional distance can increase or decrease depending on the nature of the species lost and the habitat type of the comparative community.

An analysis using Residual Diversity can allow the habitat of the base fauna to be identified as well as assisting in the recognition of biases resulting from species loss and the converse, the lack of bias in faunas. There are four significant characters which are important for the interpretation of residual diversity patterns:

i. Height of the scatter of points on the vertical (De) axis.

ii. Degree of displacement along the horizontal (Dp) axis.

iii. Relative positions of the different habitat groups.

iv. Relative positions of individual communities within the different habitat groups.

To these must be added two more characters which become important as species are lost during simulations or fossilization:

v. Relative movement of habitat groups on the horizontal and vertical axes.

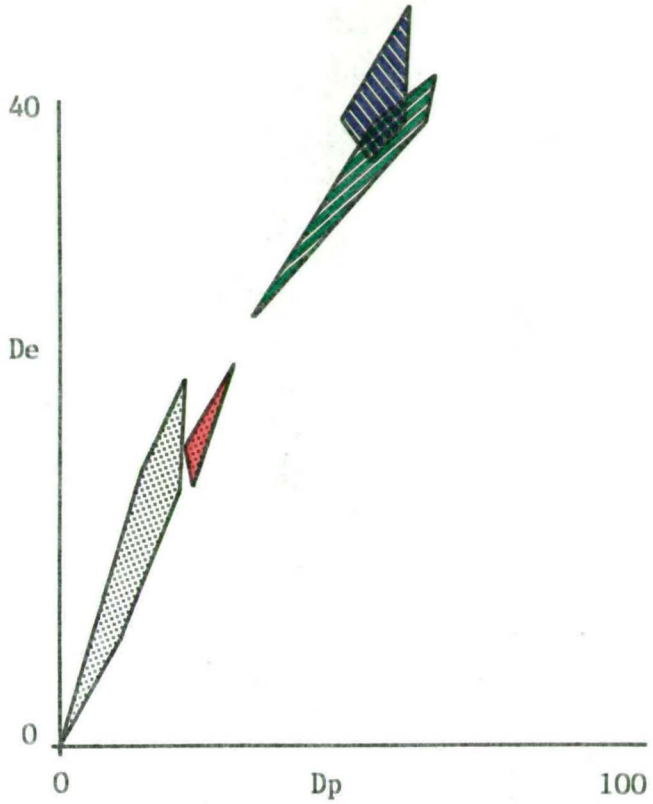
vi. Relative movement of communities within habitat groups.

In the simulations which follow, the conditions are kept as similar as possible to those in the THI simulations described earlier in the chapter. The same communities are used and the same species removed, in the same order. Residual diversity patterns are described in terms of habitat groups alone. The relative positions of individual communities within groups and their movements during species loss (characters iv and vi) are not discussed.

a. Tropical habitats.

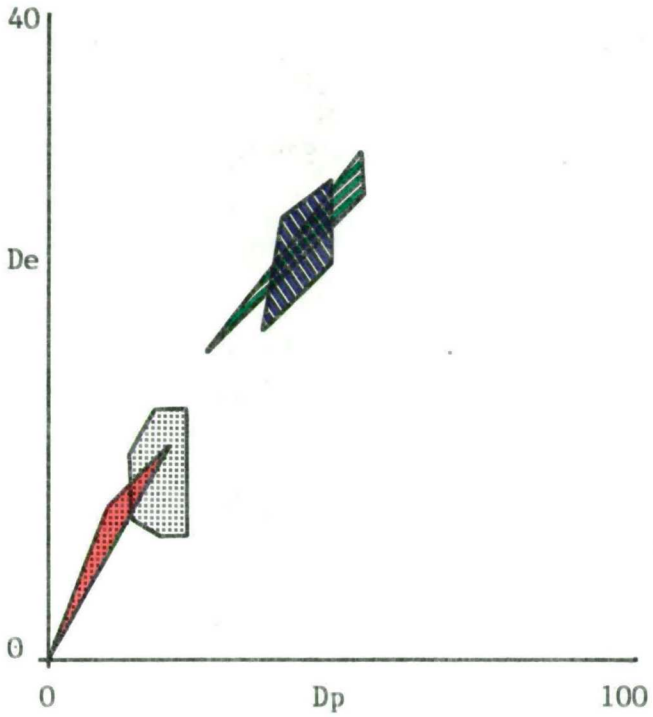
The unbiased patterns of four tropical habitat types are described (forest type I, forest type II, woodland-bushland and grassland/floodplain). Communities from these habitat are subjected to the two types of simulation described above (removal of small-bodied and large-bodied species). A key to residual diversity patterns is to be found in appendix 5.

Figure 5.26. Residual diversity pattern of a forest type I community.



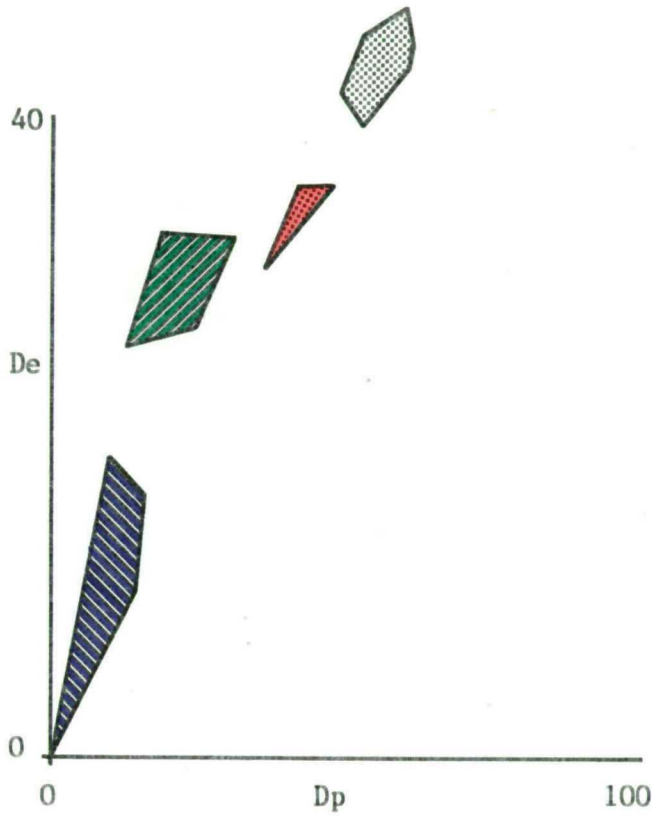

In the forest type I pattern, the group of forest type I communities lies nearest the origin with the forest type II group next to it. In general, the forest type I communities have lower Dp and De values than the forest type II communities. The grassland and woodland-bushland groups are further from the origin. These two groups share similar Dp values and hence overlap on the horizontal axis. The woodland-bushland group has, on average, higher De values and lies largely above the grassland group. This pattern shows that the forest type I base fauna is most similar to other forest type I communities. It is also similar to forest type II communities, but is least similar to grassland and woodland-bushland communities.

Figure 5.27. Residual diversity pattern of a forest type II community.



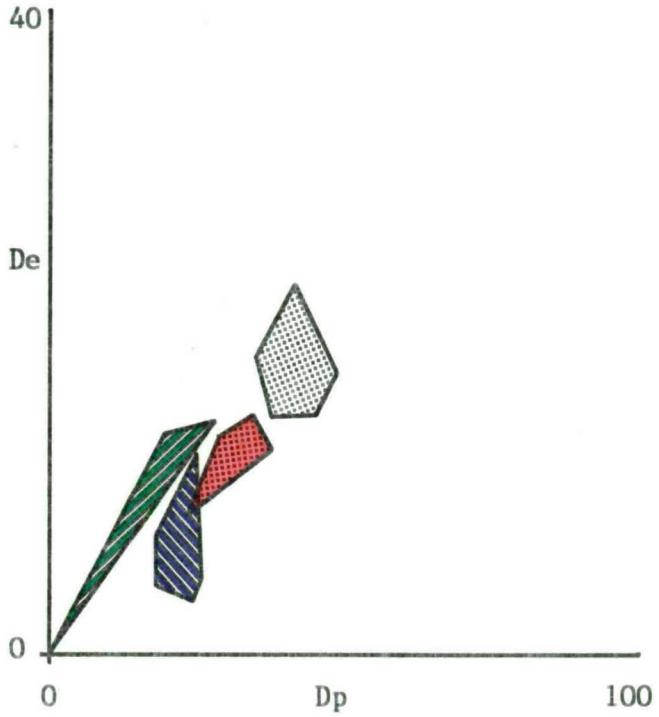

The forest type II pattern has the group of forest type II communities nearest the origin. The forest type I group lies above and to the right of this first group, overlapping the upper end. The woodland-bushland and grassland groups groups lie further from the origin, overlapping in their mid-parts and thus sharing similar De and Dp values. This residual diversity pattern shows that the forest type II base fauna is most similar in structure to other forest type II communities and slightly less similar to forest type I communities. The forest type II base fauna is least similar to woodland-bushland and grassland communities.

Figure 5.28. Residual diversity pattern of a woodland-bushland community.




In the unbiased residual diversity pattern of this woodland-bushland community the group of woodland-bushland communities lies nearest the origin, while the grassland group lies above this first group with similar Dp values but higher De values. The forest type II group lies above and slightly to the right of the grassland group. The forest type I group is above and still further to the right of the forest type II group. The woodland-bushland base fauna is clearly most similar in structure to the woodland-bushland group of communities, while grassland is the next most similar community type. There is apparently no close resemblance to the type of structure shown by forest communities, although there is slightly more similarity to type II communities than to those of the type I group.

Figure 5.29. Residual diversity pattern of a grassland/floodplain community.




In the unbiased residual diversity pattern of this habitat type, the woodland-bushland and grassland groups share similar De values. The group of woodland -bushland communities has slightly higher Dp values and thus lies to the right of the grassland group, which is closest to the origin. The forest type II group falls to the right and largely above the woodland-bushland group. The forest type I group is still further above and to the right of the type II group. The groups of woodland-bushland and grassland communities appear to be equally similar to the grassland base fauna in structre. The forest type II communities also show some similarity, while the least similarity overall is shown by the forest type I communities.

Residual diversity simulations: Tropical habitats.

Forest type I.

Figure 5.30. Small-bodied species removed.

As species are removed, any excesses which the base fauna has compared with the modern comparative communities are reduced and, as a consequence, the De values of all groups fall steadily throughout the simulation. At the same time the Dp values of the groups also increase. In the unbiased state, the lowest Dp values are shown by the group of forest type I communities, but by the end of the simulation these communities have the highest Dp values. This group shows great rightward displacement during the simulation and a similar trend is shown by the forest type II group. The woodland-bushland and grassland groups show relatively little movement to the right and the majority of their motion is vertically downwards. In the final pattern, while all four groups share similar De values, the lowest Dp values are shown by the group of woodland-bushland communities, followed by the grassland, forest type II and forest type I groups in order of increasing Dp values.

This simulation series demonstrates that although forest communities are the most similar to the base fauna at the outset, the removal of small-bodied species changes this relationship. The structure of the base fauna becomes progressively less similar to that of forest communities and relatively more similar to the structure found in woodland-bushland and grassland communities, although the overall similarity to modern communities is reduced.

Figure 5.30.

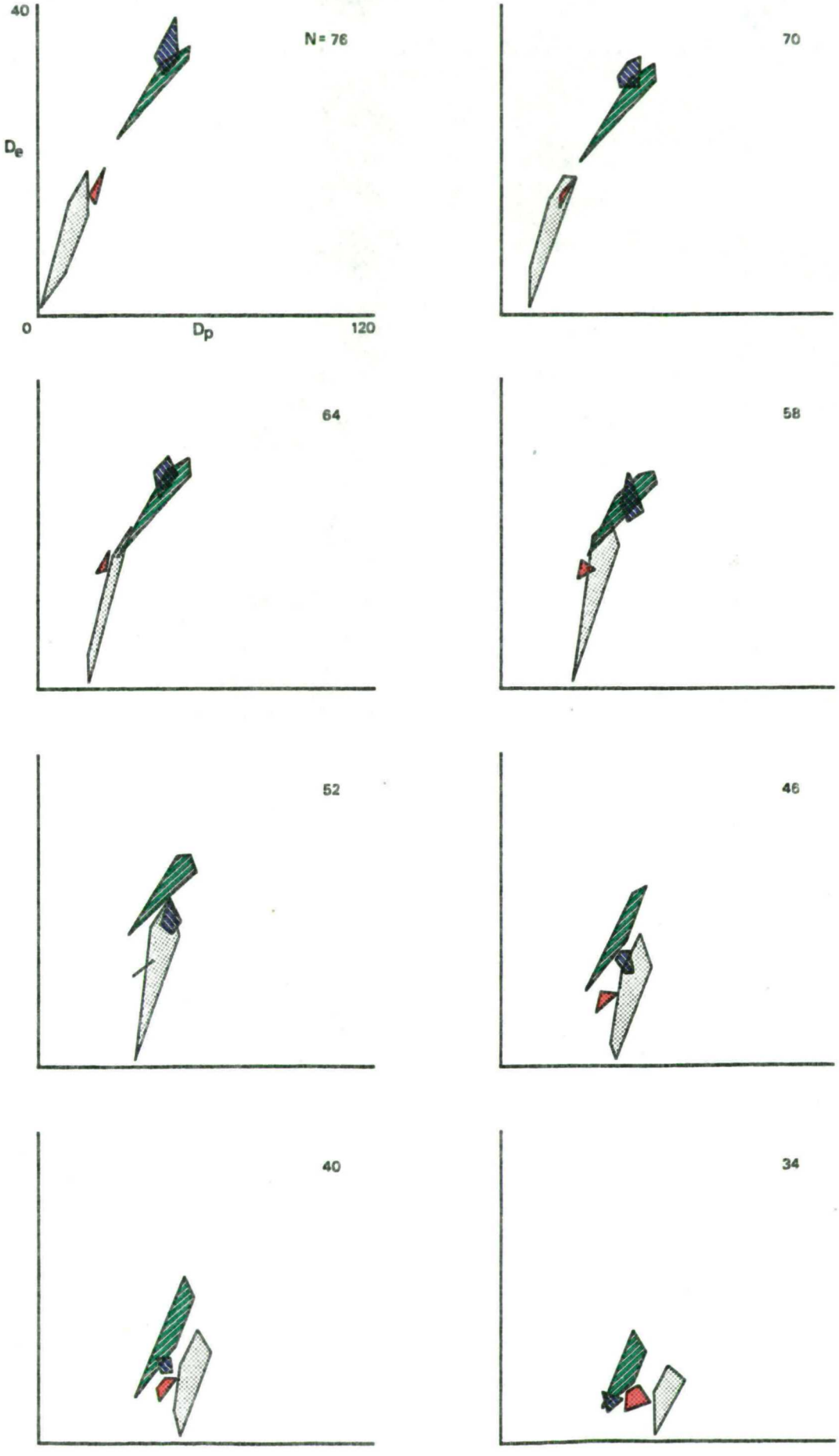
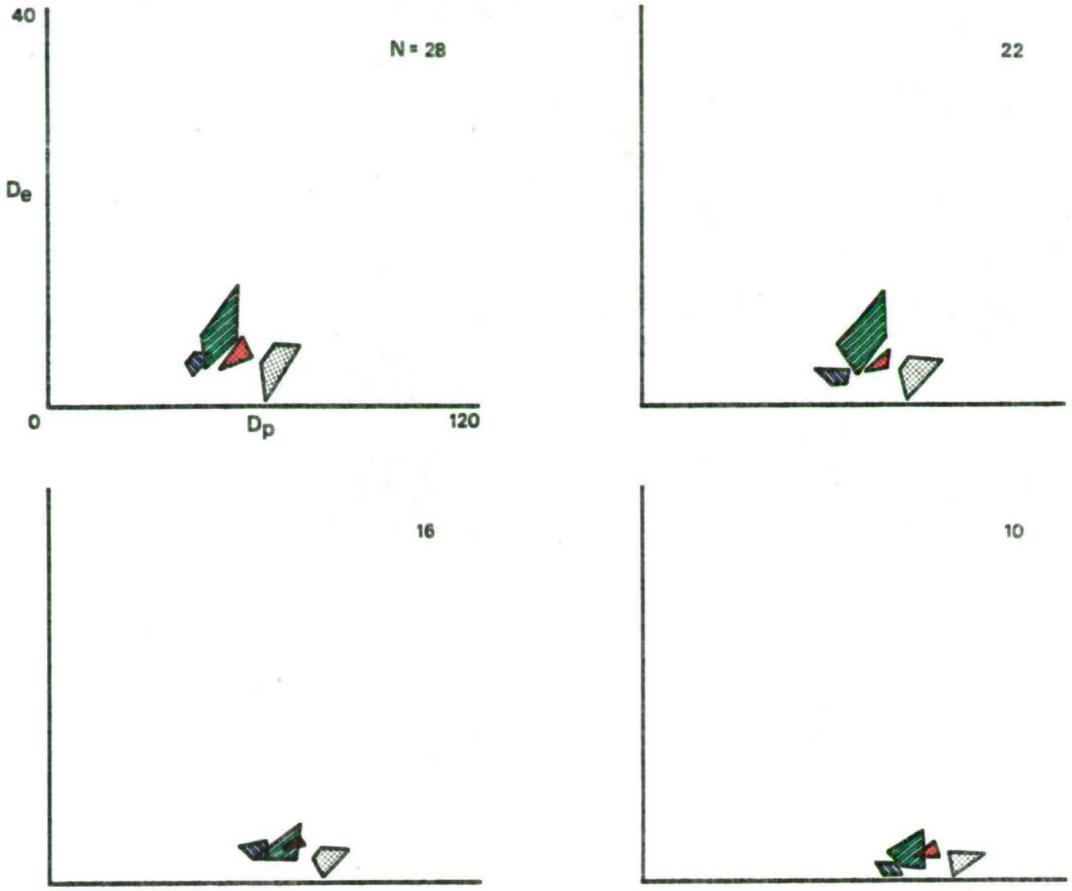


Figure 5.30. (cont.)



Residual diversity simulations: Tropical habitats.

Forest type I.

Figure 5.31. Large-bodied species removed.

The initial effect of removing large-bodied species is a general movement of all habitat groups to the right, corresponding to a general increase in Dp values. Later in the simulation increasing vertical movement by the four groups becomes more important as De values are gradually decreased. The grassland group shows relatively less movement downwards and to the right than the woodland-bushland group, but apart from this and in spite of the general trends downwards and to the right, the relative positions of the four groups remains fairly constant throughout.

The removal of large-bodied species evidently makes the base fauna progressively less like any complete modern community. However, in spite of this, the base fauna remains more similar overall to forest communities than to woodland-bushland and grassland communities.

Figure 5.31.

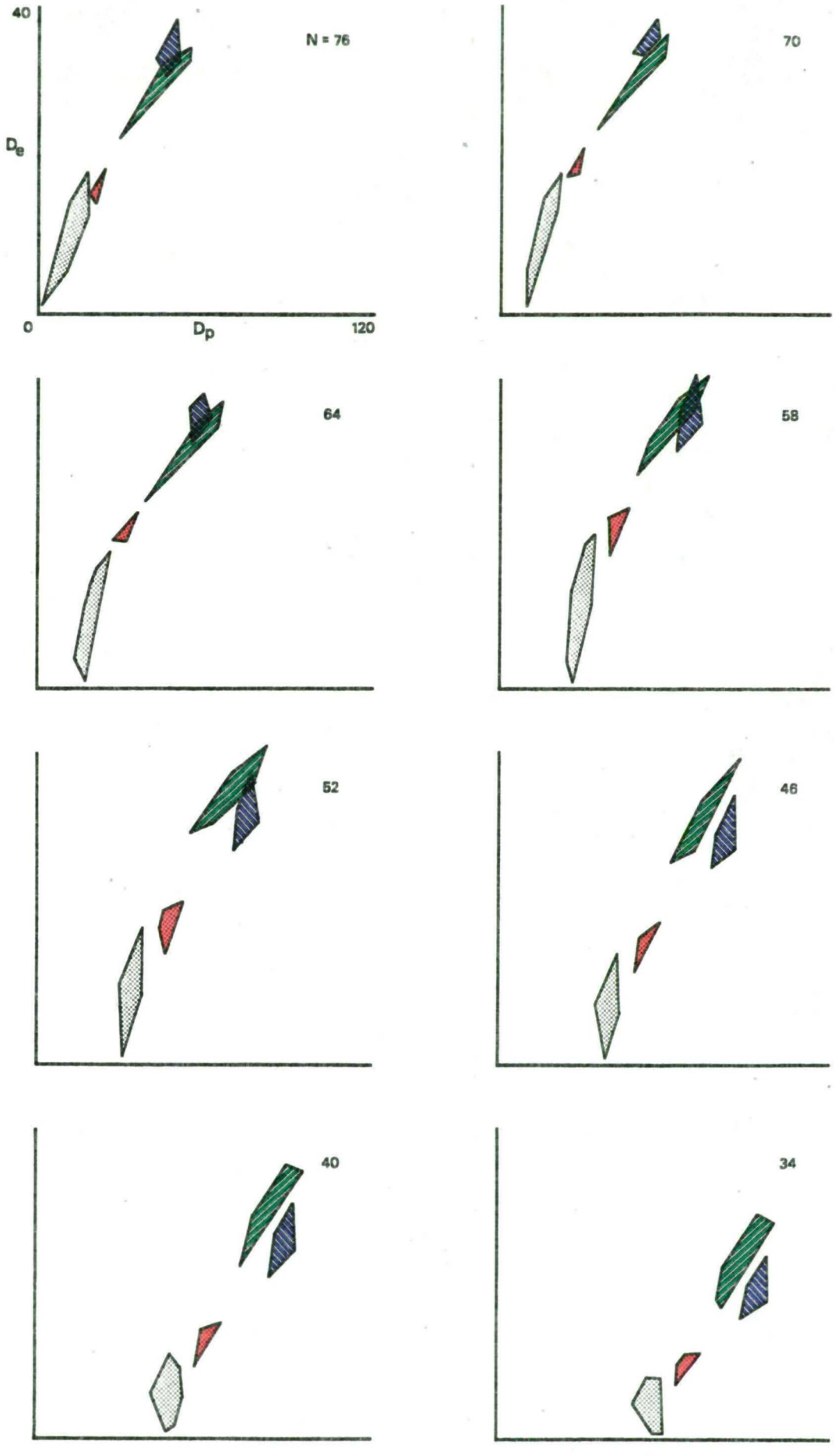
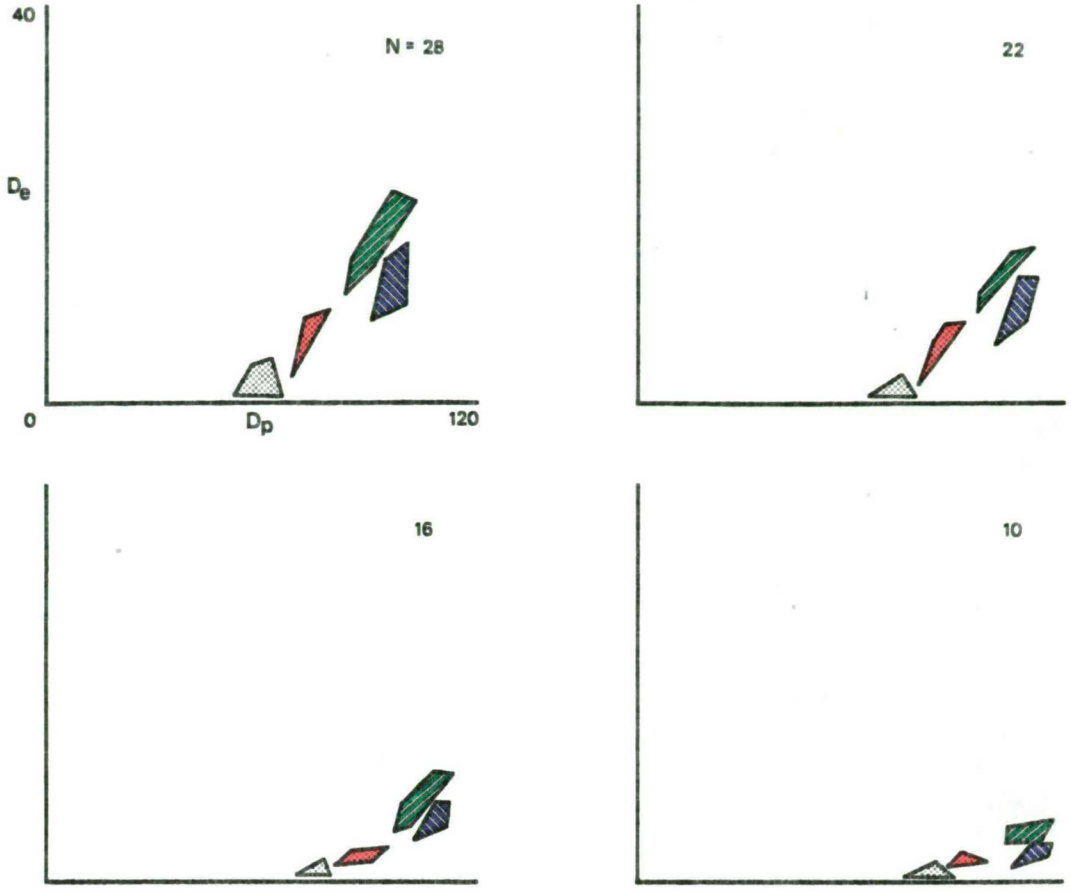


Figure 5.31. (cont.)



Residual diversity simulations: Tropical habitats.

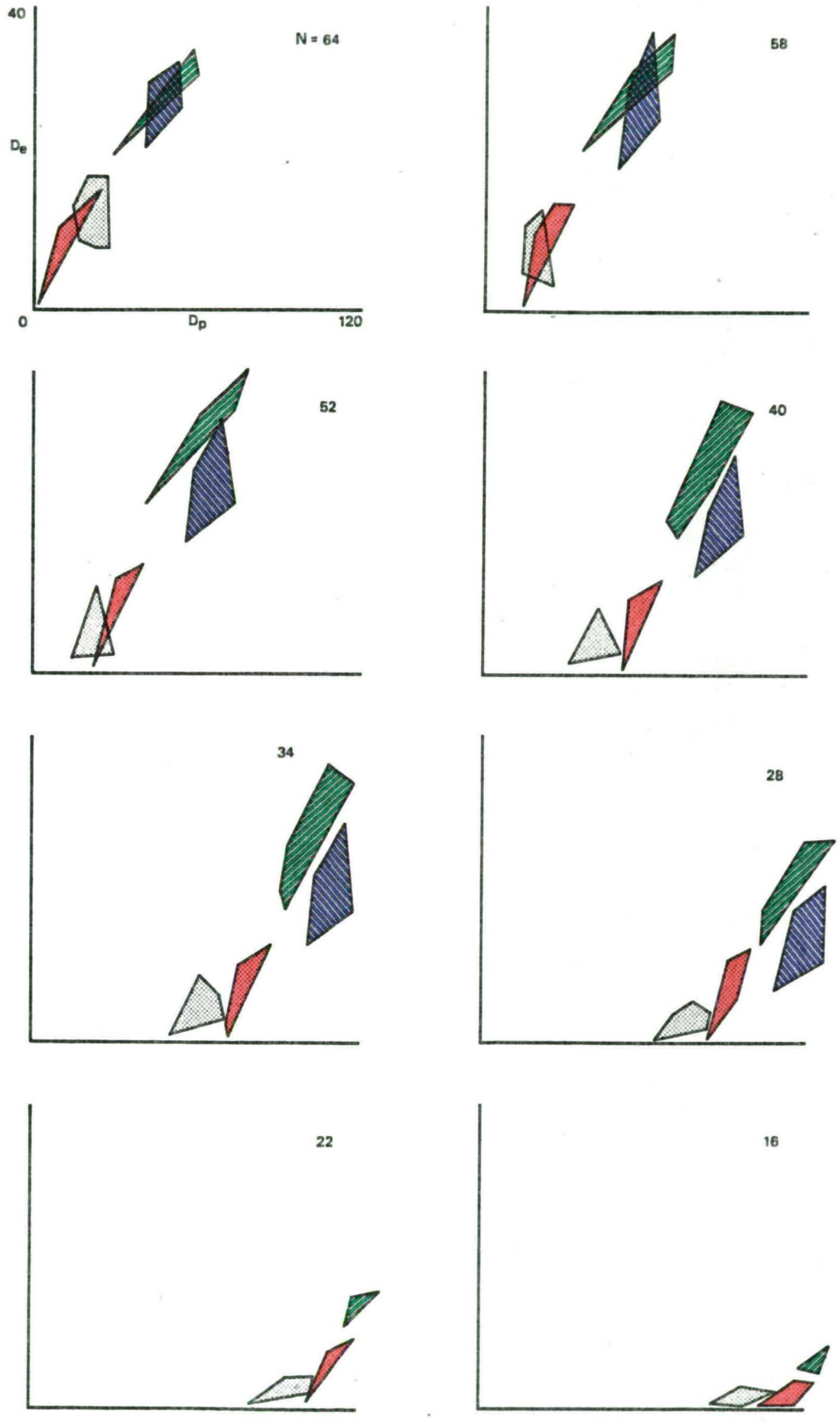
Forest type II.

Figure 5.32. Small-bodied species removed.

All four habitat groups show movement downwards and to the right during the course of this simulation, but the two forest groups show relatively greater movement than the non-forest groups. The forest groups overlap at first, but the forest type I group shows the greatest increase in Dp values and ends the simulation further from the origin than the forest type II group. The two non-forest groups show less increase in their Dp values but greater reduction of De values so that most of their movement is vertically downwards. By the end of the simulation all four groups share similar De values, but the woodland-bushland and grassland groups lie nearest the origin.

The structure of the base fauna is initially most similar to that of forest type II communities. The removal of small-bodied species makes the base fauna less like the forest communities and increases the relative similarity to non-forest communities.

Figure 5.32.



Residual diversity simulations: Tropical habitats.

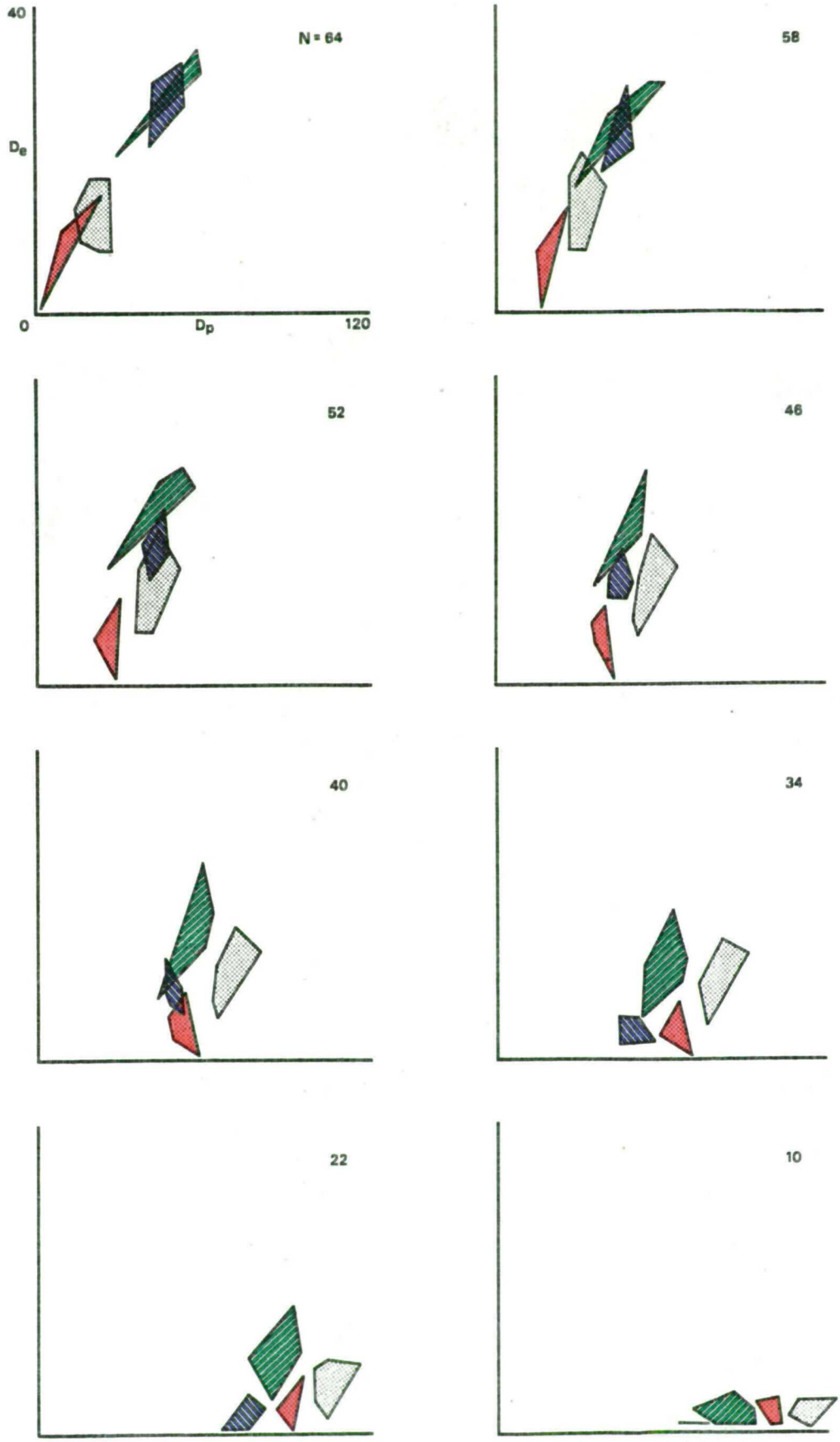
Forest type II.

Figure 5.33. Large-bodied species removed.

During the course of this simulation the position of the two forest groups relative to the woodland-bushland and grassland groups remains fairly constant. The forest type II group shows slightly greater displacement to the right than the forest type I group, while the woodland-bushland groups shows slightly more rightward displacement than the grassland group, and all four groups show a gradual vertical collapse as their De values decline.

The initial similarity of the base fauna to forest type II communities is not preserved and by the end of the simulation the base fauna appears to be more similar in structure to forest type I communities. However, although the overall similarity to modern communities is reduced, the base fauna does remain more similar to forest communities than to woodland-bushland or grassland communities.

Figure 5.33.



Residual diversity simulations: Tropical habitats.

Woodland-bushland.

Figure 5.34. Small-bodied species removed.

The relative positions of the four groups is preserved despite the gradual vertical collapse and displacement to the right which affects the whole pattern. At the end of the simulation the four groups have similar De values, but the woodland-bushland and grassland groups still share similar Dp values, while the two forest groups lie further from the origin with higher Dp values.

This simulation shows that as small-bodied species are removed from the woodland-bushland base fauna, its overall similarity to modern communities is reduced, but it still remains more similar to woodland-bushland than to forest communities.

Figure 5.34.

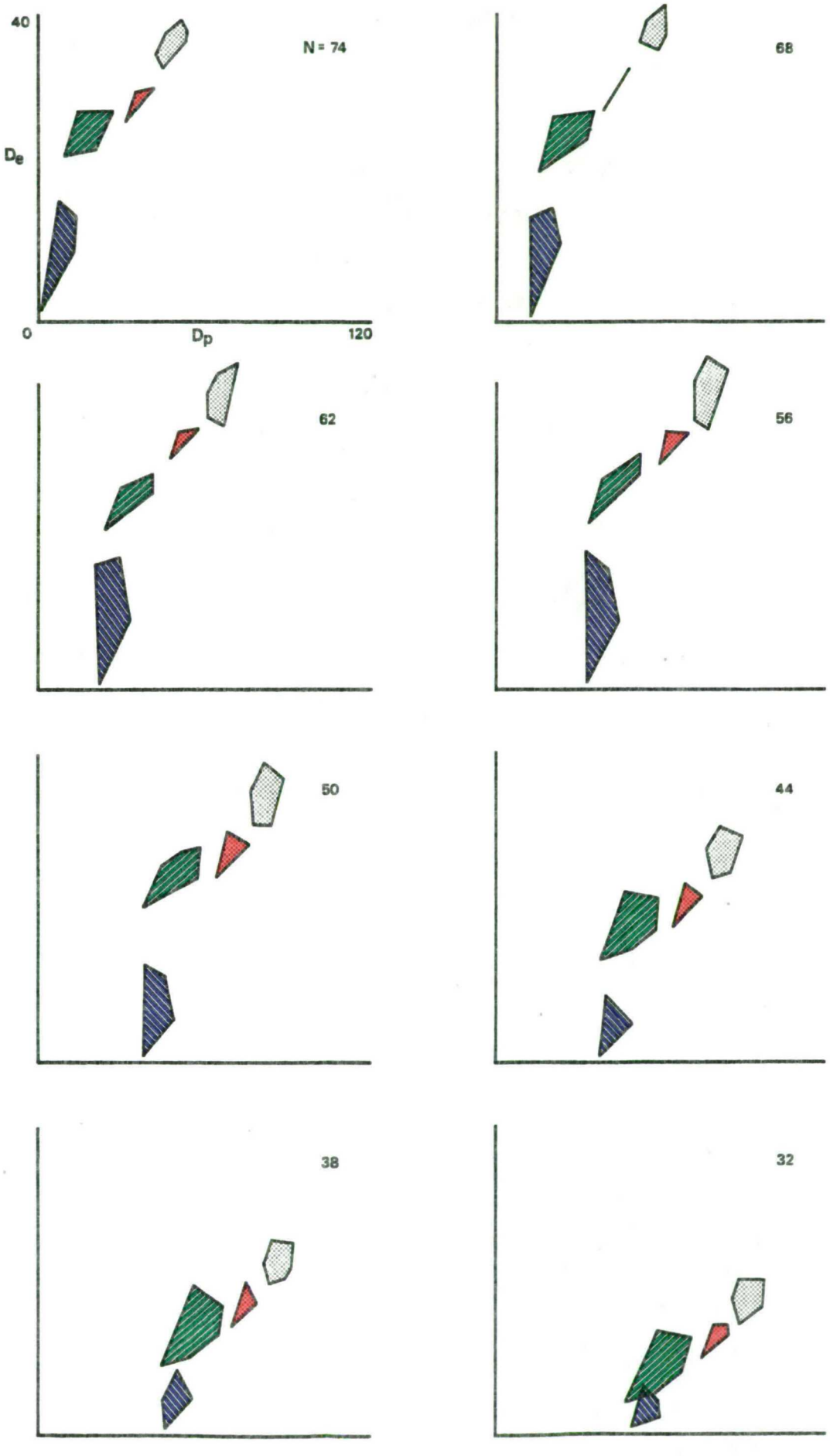
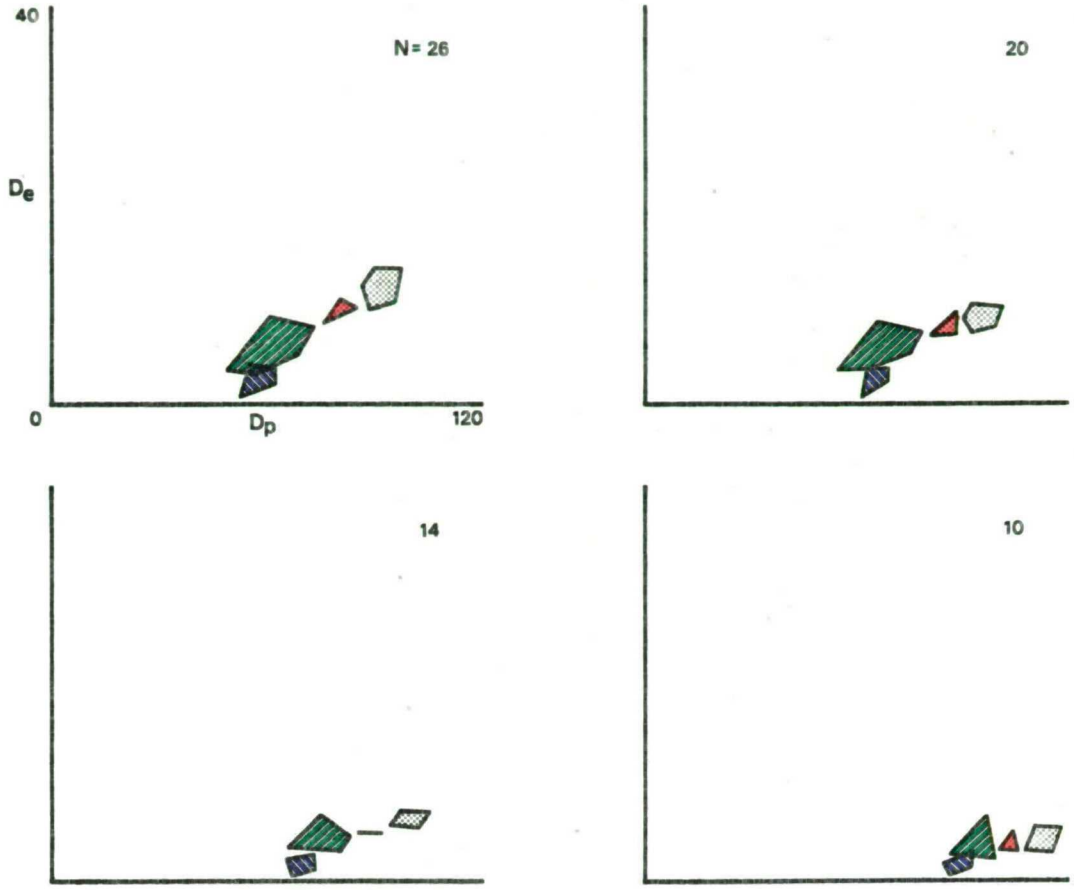


Figure 5.34. (cont.)



Residual diversity simulations: Tropical habitats.

Woodland-bushland.

Figure 5.35. Large-bodied species removed.

During the course of this simulation all four groups show vertical collapse as De values fall. The grassland and woodland-bushland groups also undergo a large displacement to the right. The two forest groups do not show any movement to the right at first and fall vertically before moving away from the origin only at the end of the sequence. The grassland and woodland-bushland groups have similar Dp values throughout and the grassland group maintains a slightly higher De value. The forest type I group, which initially has the highest Dp values, shows the least displacement to the right and hence finishes nearest the origin. The final pattern shows both the forest groups to the left of the two non-forest groups.

The base fauna is initially most similar to modern communities from woodalnd-bushland habitats, but the removal of large-bodied species reduces this similarity. The base fauna becomes less like any modern community, but it also becomes relatively more similar in structure to modern forest communities than to those from woodland-bushland and grassland habitats.

Figure 5.35.

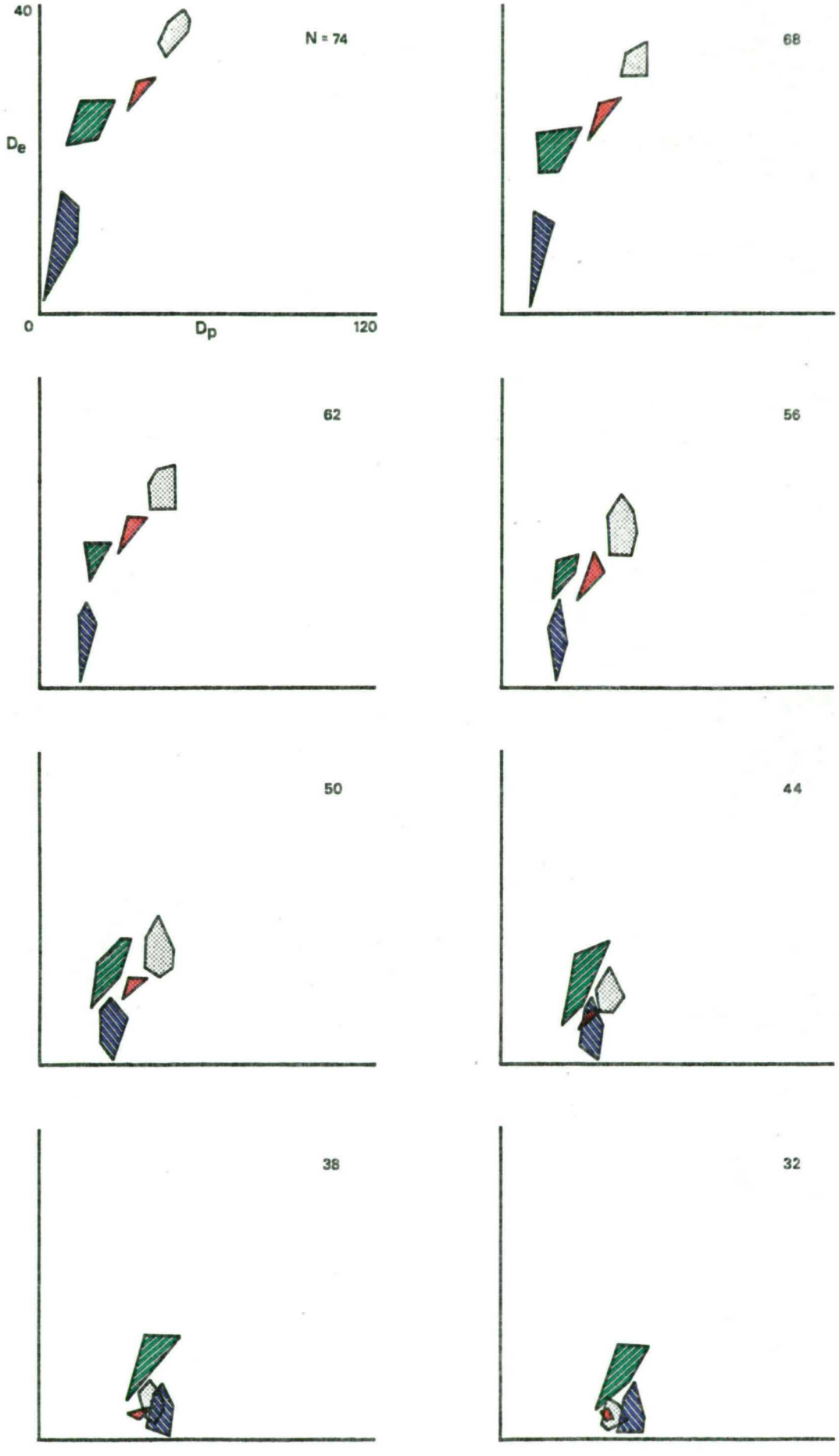
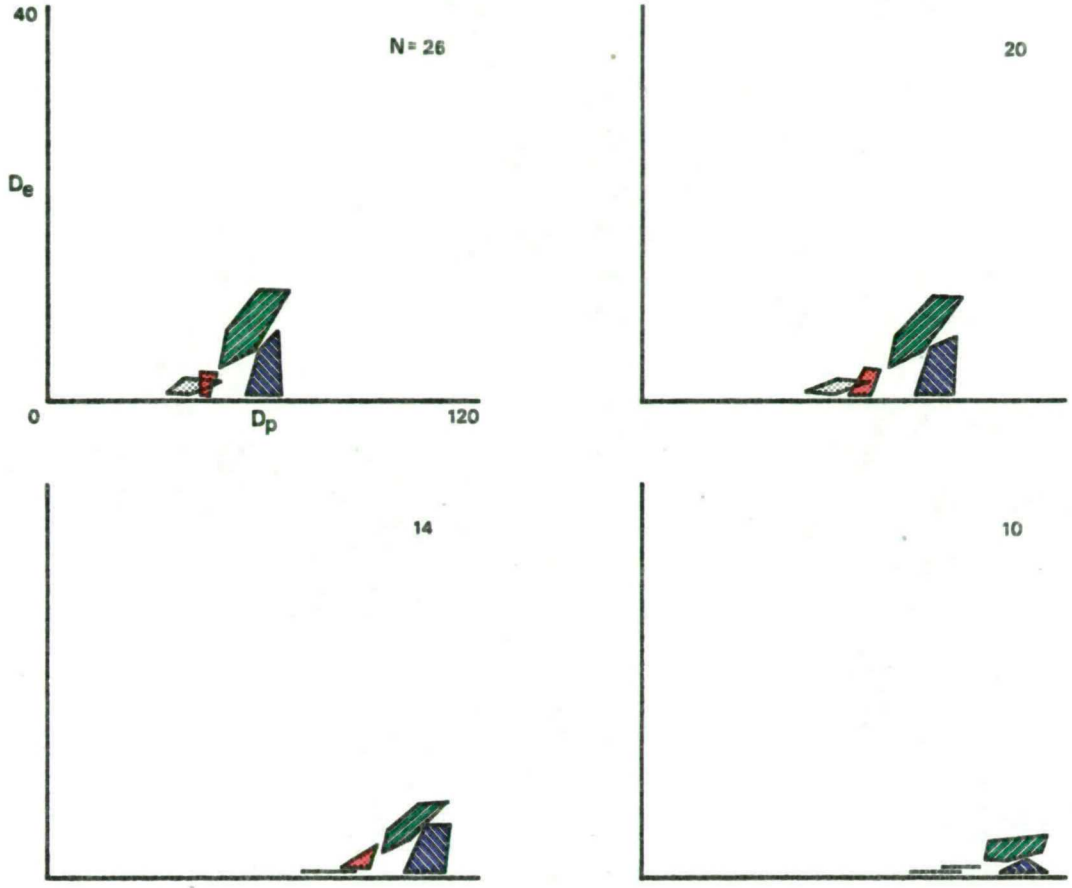


Figure 5.35. (cont.)



Residual diversity simulations: Tropical habitats.

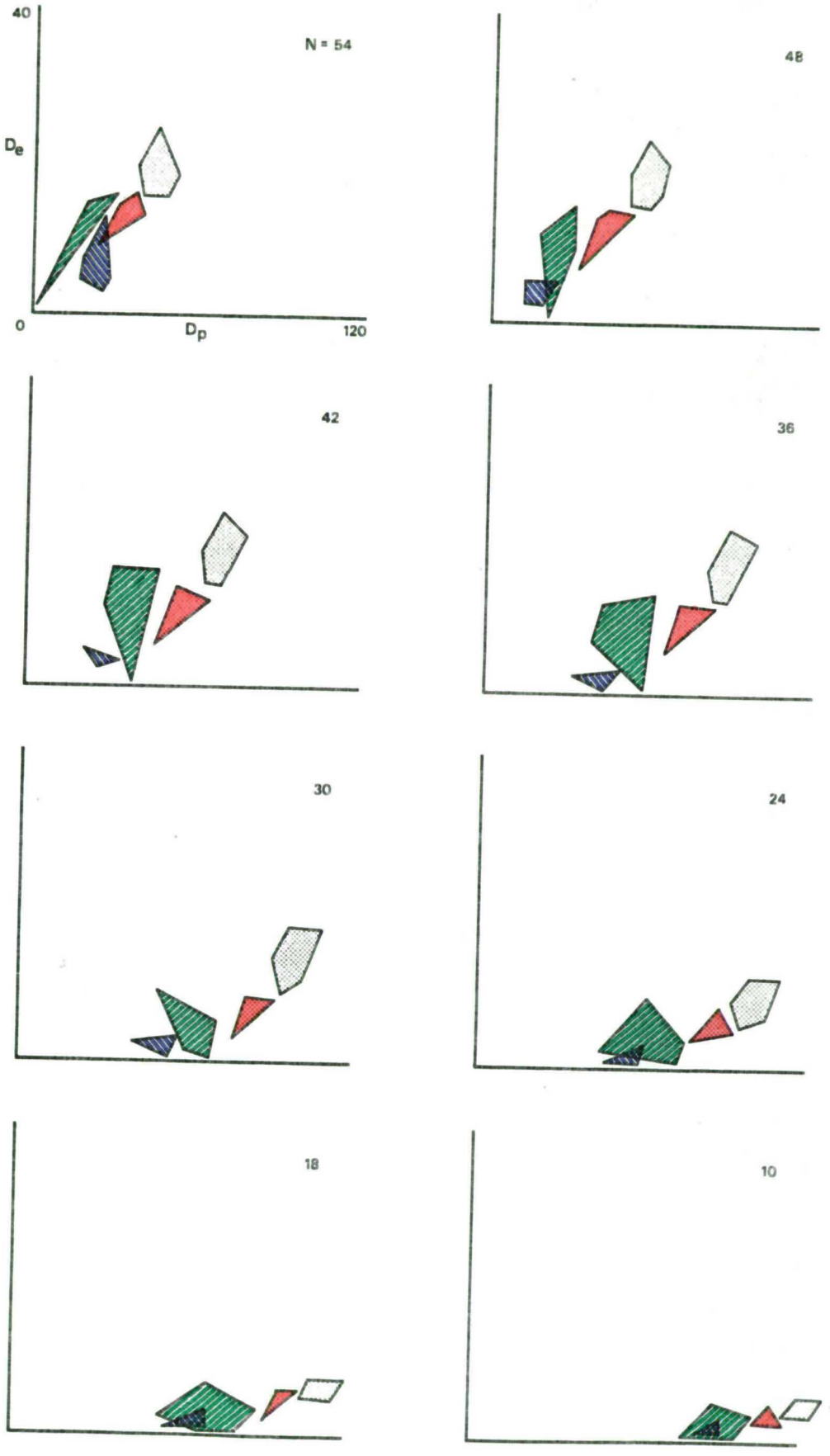
Grassland.

Figure 5.36. Small-bodied species removed.

With the removal of small-bodied species, the relation between the two forest groups and the two non -forest groups remains fairly constant, although the De values of all the groups becomes similar towards the end of the sequence. The relationship between the grassland and woodland-bushland groups changes during the course of the simulation. At first, the woodland-bushland group lies to the right of the grassland group. These positions are reversed in the mid-part of the sequence, but by the end, the two groups overlap completely. The De values of the woodland-bushland communities also fall more rapidly than those of the grassland group, but by the end of the simulation the De values of the two groups have become more or less equal again.

The removal of small-bodied species reduces the overall similarity of the base fauna to modern communities, but does not alter the greater resemblance of the base fauna to modern non-forest communities than to forest communities.

Figure 5.36.



Residual diversity simulations: Tropical habitats.

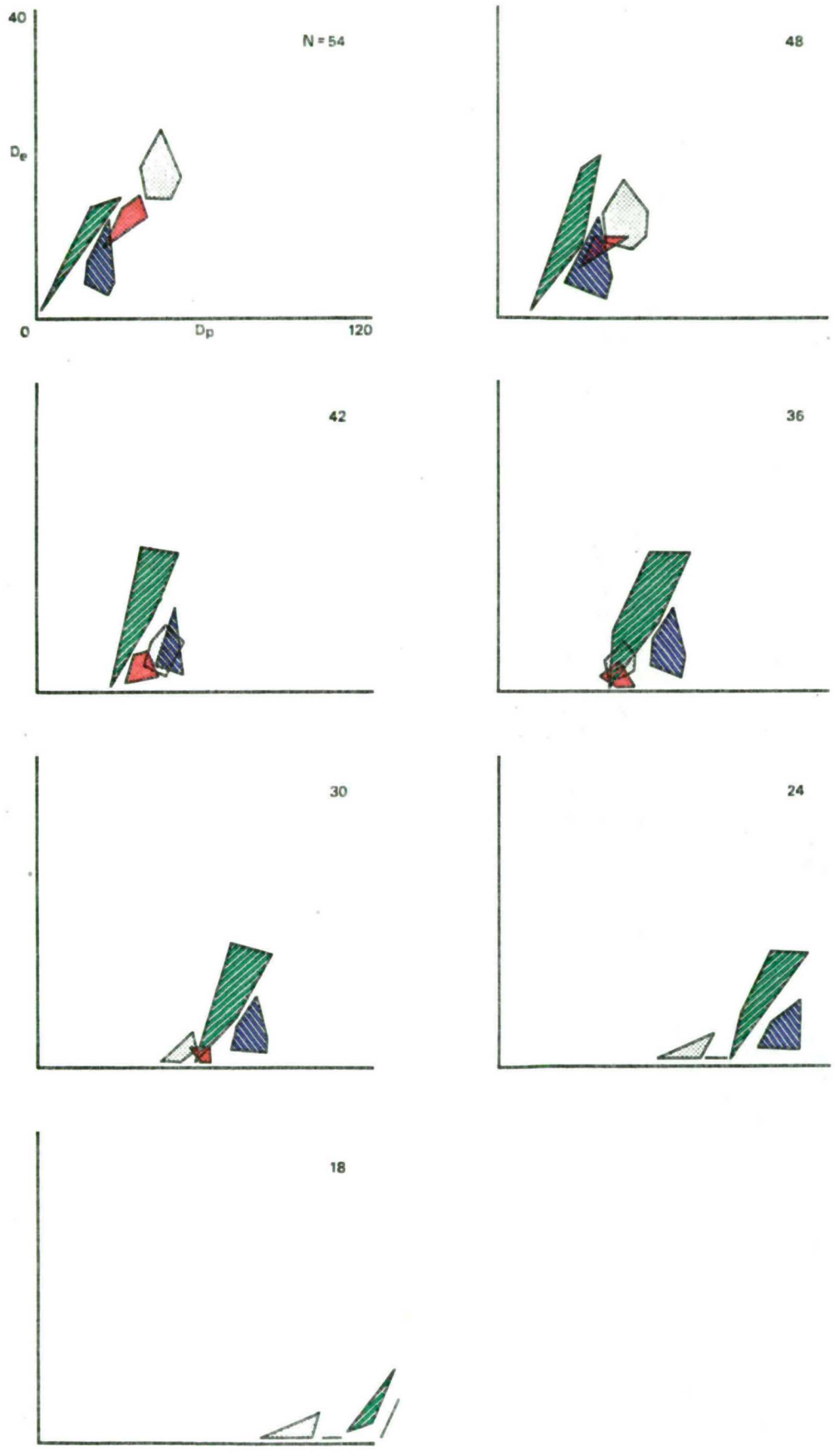
Grassland.

Figure 5.37. Large-bodied species removed.

Within the general trend for groups to move downwards and to the right, the forest groups show less movement than the two groups of communities from non-forest habitats. While the woodland-bushland and grassland groups move downwards and to the right throughout, the two forest groups show no rightward displacement at first and drop vertically before moving away from the origin only at the end of the simulation. The forest type I group, which starts with the highest Dp value, finishes with the lowest, while the two non-forest groups, which start with the lowest Dp values, maintain their positions relative to each other but finish the simulation with the highest Dp values.

The unbiased base fauna is most similar to non-forest communities from woodland-bushland and grassland habitats, but the removal of large-bodied species converts the structure of the base fauna until it is more like that found in forest communities.

Figure 5.37.



Conclusions.

Figures 5.38 and 5.39 illustrate the final patterns resulting from the simulation series described above. Figure 5.38 shows the final patterns of the four series in which small-bodied species were removed, and figure 5.39 shows the final patterns resulting from the removal of large-bodied species. It can be seen that the simulations tend to converge on two patterns. The removal of small-bodied species results in a base fauna dominated by large-bodied forms. This has a residual diversity pattern in which the relative positions of the four habitat groups resembles that found in non-forest communities (compare figure 5.38 with figures 5.28 and 5.29). The removal of large-bodied species results in a base fauna whose structure gives a residual diversity pattern most similar to that found in forest communities (compare figure 5.39 with figures 5.26 and 5.27). Table 5.1 summarizes the effects of the two types of simulation on communities from the four tropical habitat types.

Figure 5.38. Residual diversity simulations: Tropical habitats: Final patterns resulting from the removal of small-bodied species.

This figure shows the final patterns resulting from the four simulations in which small-bodied species were removed. All four simulations converge on a final residual diversity pattern which is most similar to that for non-forest communities, in which the grassland and woodland-bushland groups are closest to the origin.

Figure 5.38.

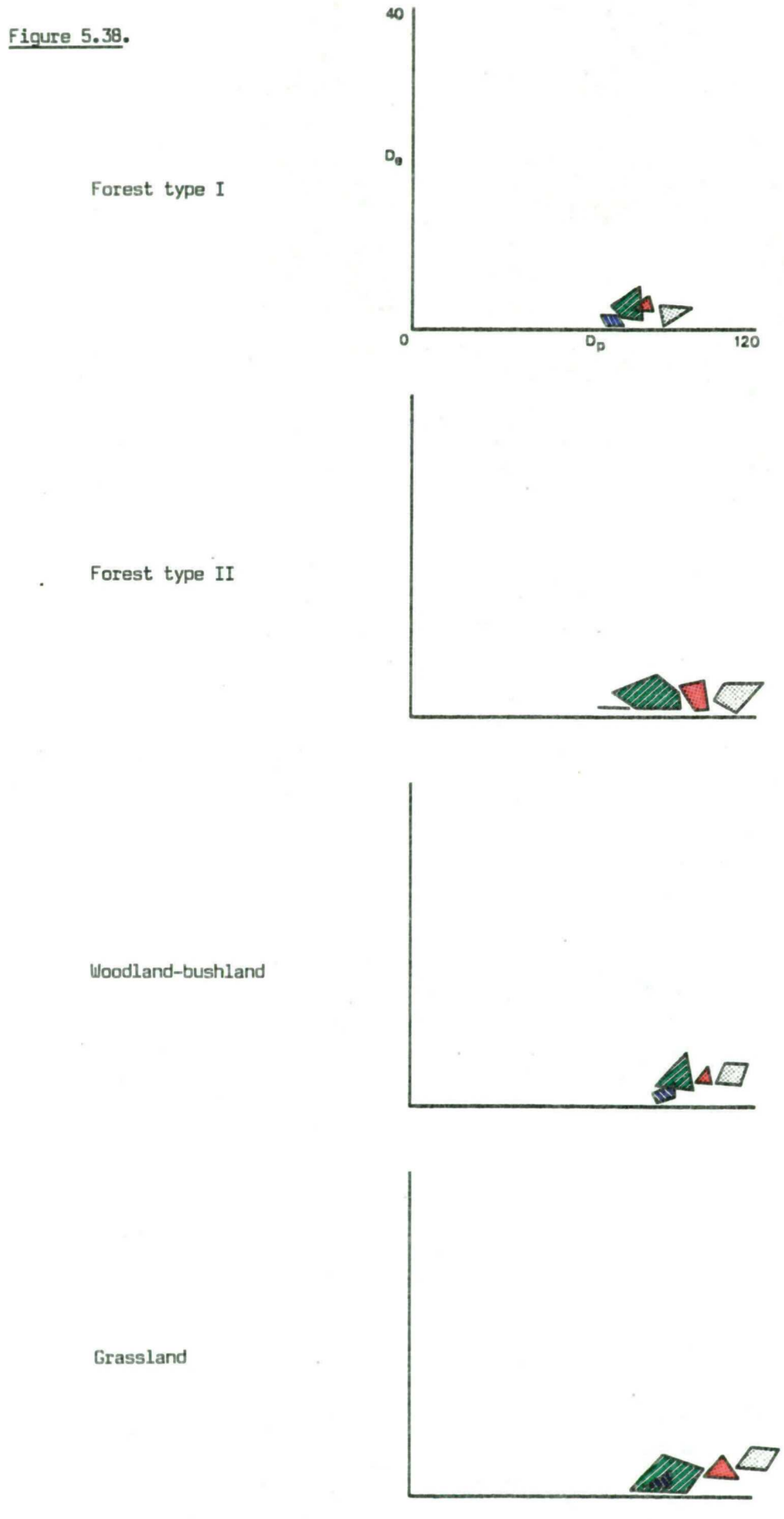
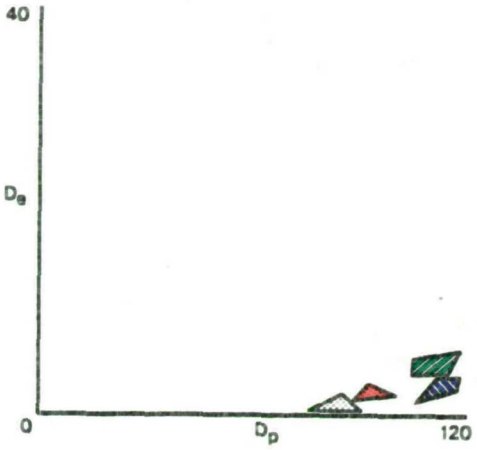

40
$D_\theta$
0
$D_p$
120
Forest type I
Forest type II
Woodland-bushland
Grassland

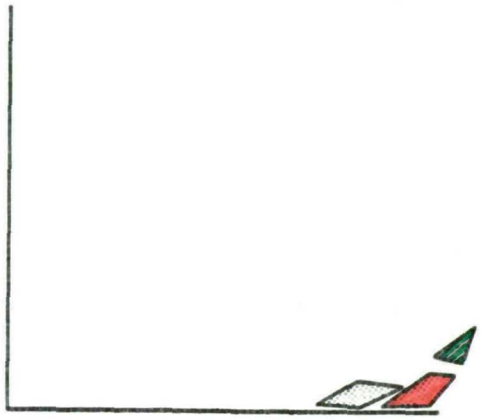
Figure 5.39. Residual diversity simulations: Tropical habitats: Final patterns resulting from the removal of large-bodied species.

This figure shows the final patterns resulting from the four simulations in which large-bodied species were removed. All four simulations converge on a final residual diversity pattern which is most similar to that of forest communities, in which the two forest groups lie nearest the origin, with the two non-forest groups to the right, further from the origin.

Figure 3.39.

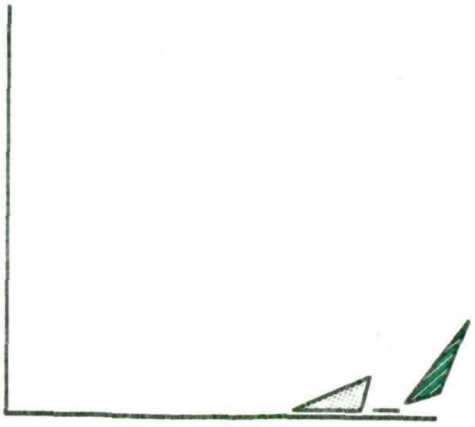



Forest type I



Forest type II

Woodland-bushland



Grassland

Table 5.1. Effects of simulations on tropical habitats.

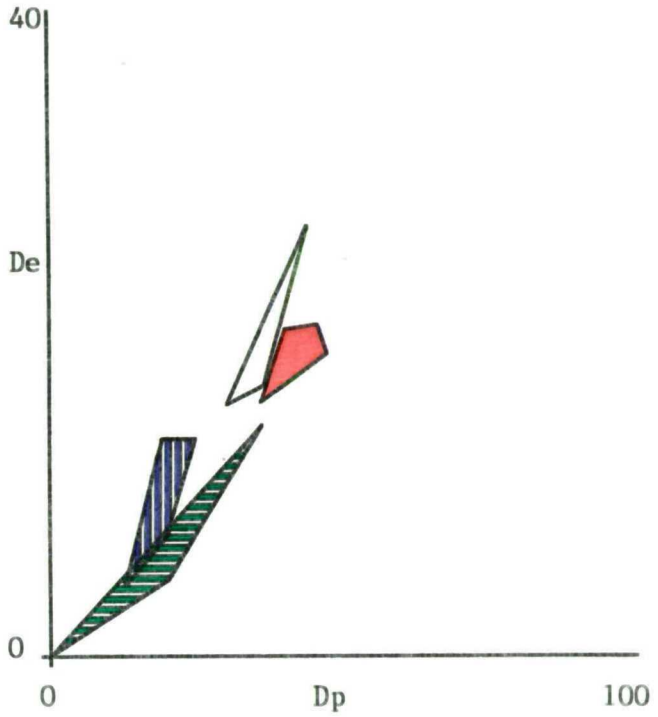
| Unbiased pattern type | Species removed | Species dominant in final fauna | Final pattern type |
|---|---|---|---|
| Forest type I | Small | Large | Non-forest |
| Forest type I | Large | Small | Forest |
| Forest type II | Small | Large | Non-forest |
| Forest type II | Large | Small | Forest |
| Woodland-bushland | Small | Large | Non-forest |
| Woodland-bushland | Large | Small | Forest |
| Grassland | Small | Large | Non-forest |
| Grassland | Large | Small | Forest |

b. Temperate habitats.

Communities from five temperate habitat types were used in the simulations that follow: Deciduous forest, boreal forest, tundra, steppe and semidesert. Simulations were not carried out on desert communities because the species richness of these is so low that they are already near the de minimis limit at which simulations are terminated (i.e. 10 species).

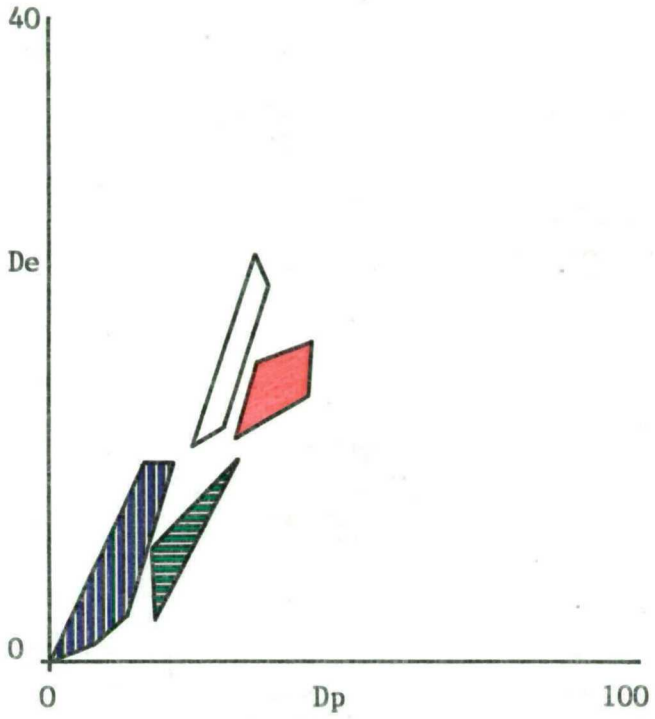
An unbiased community from each habitat is described first and then each community is subjected to two simulations, firstly, the removal of small-bodied species and secondly, the removal of large-bodied species. The unbiased residual diversity patterns of all the communities in the modern comparative sample are shown in appendix 2.

Figure 5.40. Residual diversity pattern of a deciduous forest community.



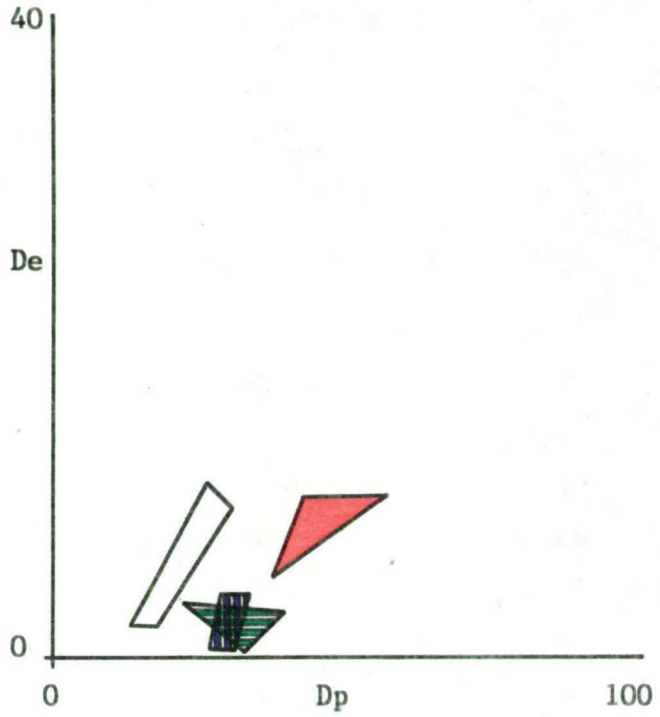

In the unbiased pattern for this deciduous forest base fauna, the boreal and deciduous forest groups lie next to each other, more or less equidistant from the origin. One of the communities is the deciduous forest group is the base fauna itself and this lies at the origin. The tundra and semidesert groups are also equidistant from the origin and lie next to each other, above and to the right of the forest groups. The Dp values of the two forest groups are similar, although the deciduous forest groups has, on average, lower De values. The tundra and semidesert groups share similar De values, but the tundra group has lower Dp values. This pattern shows that the deciduous forest base fauna is more similar in structure to communities from forest habitats than to those from non-forest habitats such as tundra and semidesert.

Figure 5.41. Residual diversity pattern of a boreal forest community.



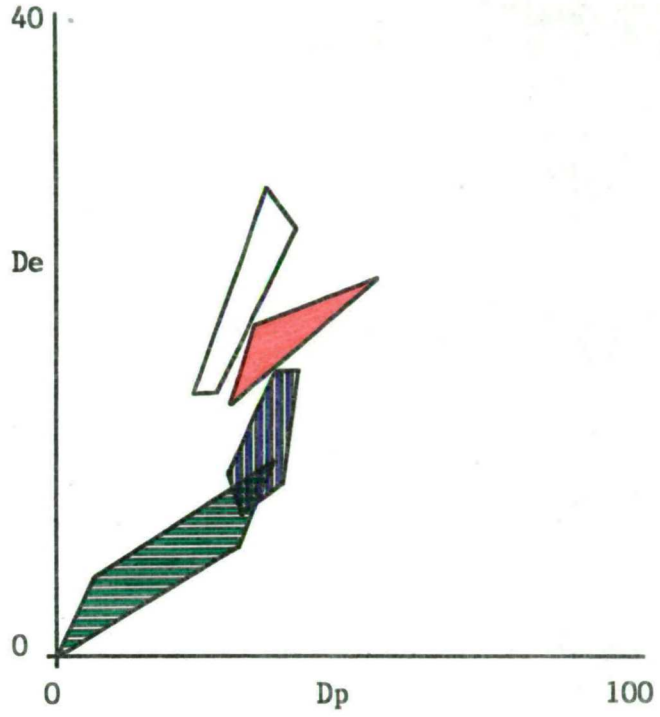

The unbiased pattern for this boreal forest community shows the boreal and deciduous forest groups lying side by side, with the boreal group slightly nearer the origin. One community of the boreal group is the base fauna and this falls at the origin. The semidesert and tundra groups lie next to each other, above and to the right of the two forest groups. The boreal and deciduous groups have similar De values, but the boreal communities tend to have lower Dp values. The tundra and semidesert groups have similar De values, but the tundra communities have lower Dp values, which are similar to those of the deciduous forest group. The boreal forest base fauna is most similar to other boreal forest communities, although it is also similar to communities of the deciduous forest group. The structure of the base fauna is not like those of tundra or semidesert communities.

Figure 5.42. Residual diversity pattern of a tundra community.



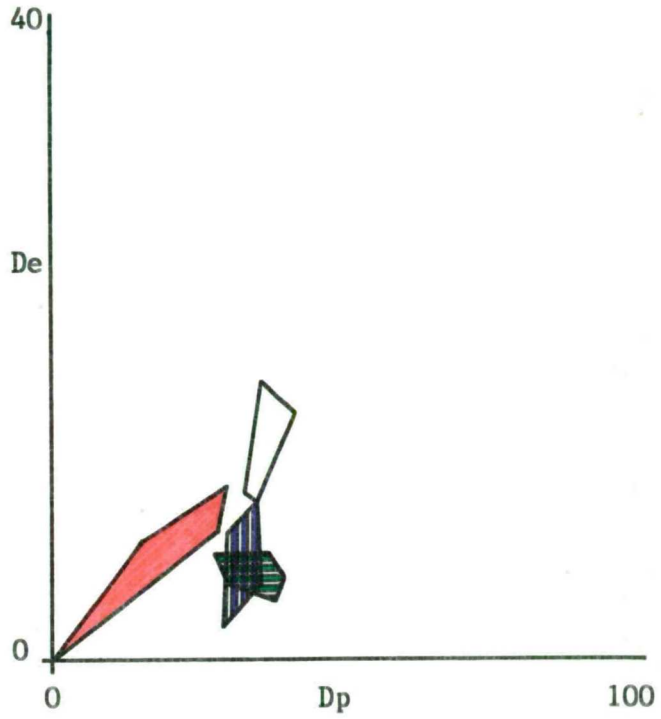

In this pattern, the tundra group of communities lies nearest the origin. The boreal and deciduous forest groups overlap each other and fall to the right of the tundra group with higher Dp values, although in general they have lower De values. The semidesert group is the most distant from the origin. This group has Dp values greater than those of any other community, but its De values are similar to those of the tundra group. This pattern shows that the community structure of the base fauna is most similar to that of other tundra communities, although communities from the two forest habitats also show some resemblance. The least similar structure is to be found among semidesert communities.

Figure 5.43. Residual diversity pattern of a steppe (forest-steppe) community.




The base fauna for this pattern is a forest -steppe community which is one of the communities in the deciduous forest group. This group lies nearest the origin with the base fauna falling at the origin. The boreal group intersects the upper part of the deciduous forest group, but in general, boreal forest communities have higher Dp and De values than deciduous forest communities. The tundra and semidesert groups are above the two forest groups, lying next to each other, with the tundra group to the left. The base fauna is clearly most similar in structure to steppe, forest-steppe and deciduous forst communities. The next most similar community type is that associated with boreal forest habitats, while the least resemblance is to tundra and semidesert communities.

Figure 5.44. Residual diversity pattern of a semidesert community.




In the unbiased pattern for this community type, the semidesert group lies nearest the origin, with one community, the base fauna, actually falling at the origin. The two forest groups are to the right of the semidesert group, intersecting in their mid-parts, with similar De values to the semidesert group, but with higher Dp values. The tundra group is furthest from the origin. It has Dp values similar to those of the forest groups, but De values greater than those of the other groups. The base fauna clearly shows most resemblance to semidesert communities. Forest communities appear to be equally dissimilar, irrespective of the actual type of forest habitat, while the least similar community structure is that shown by tundra communities.

Residual diversity simulations: Temperate habitats.

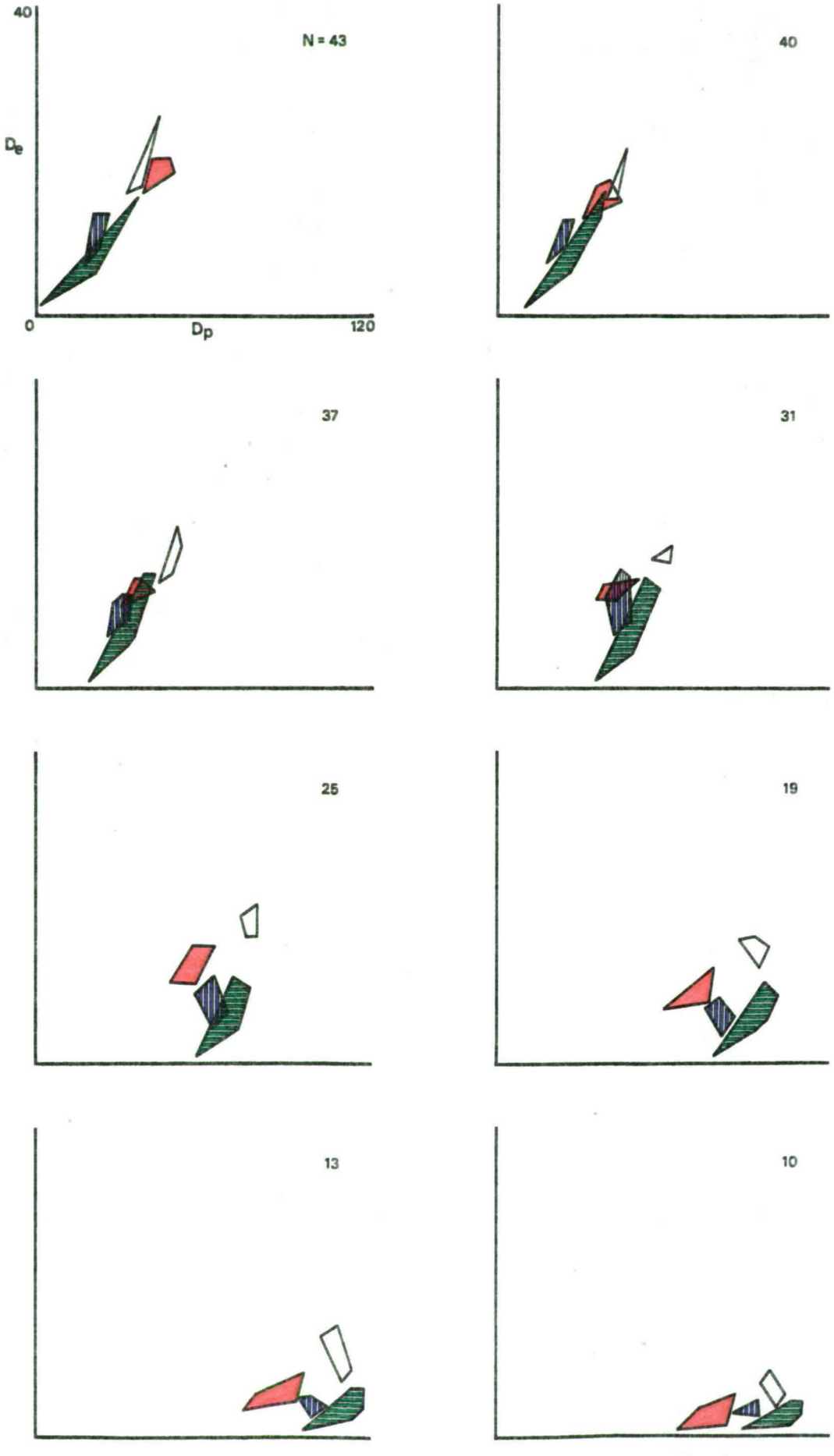
Deciduous forest.

Figure 5.45. Small-bodied species removed.

During the general movement downwards and to the right, there is a change in the relative positions of the four habitat groups. The greatest movement is seen in the two forest groups which nevertheless maintain their positions relative to each other. The tundra group keeps its position above and to the right of these two groups at first, but it then moves to take up a position directly above them. The semidesert group starts furthest from the origin, but ends the simulation as the group nearest the origin. Thus, during the simulation, the relative position of this group changes as it crosses the other groups.

This simulation shows that the base fauna is initially most similar in structure to the two groups of communities associated with forest habitats. However, as small-bodied species are removed from the base fauna, the degree of similarity to all modern communities is reduced, but at the same time, the structure of the base fauna changes so that it shows most resemblance to the semidesert communities.

Figure 5.45.



Residual diversity simulations: Temperate habitats.

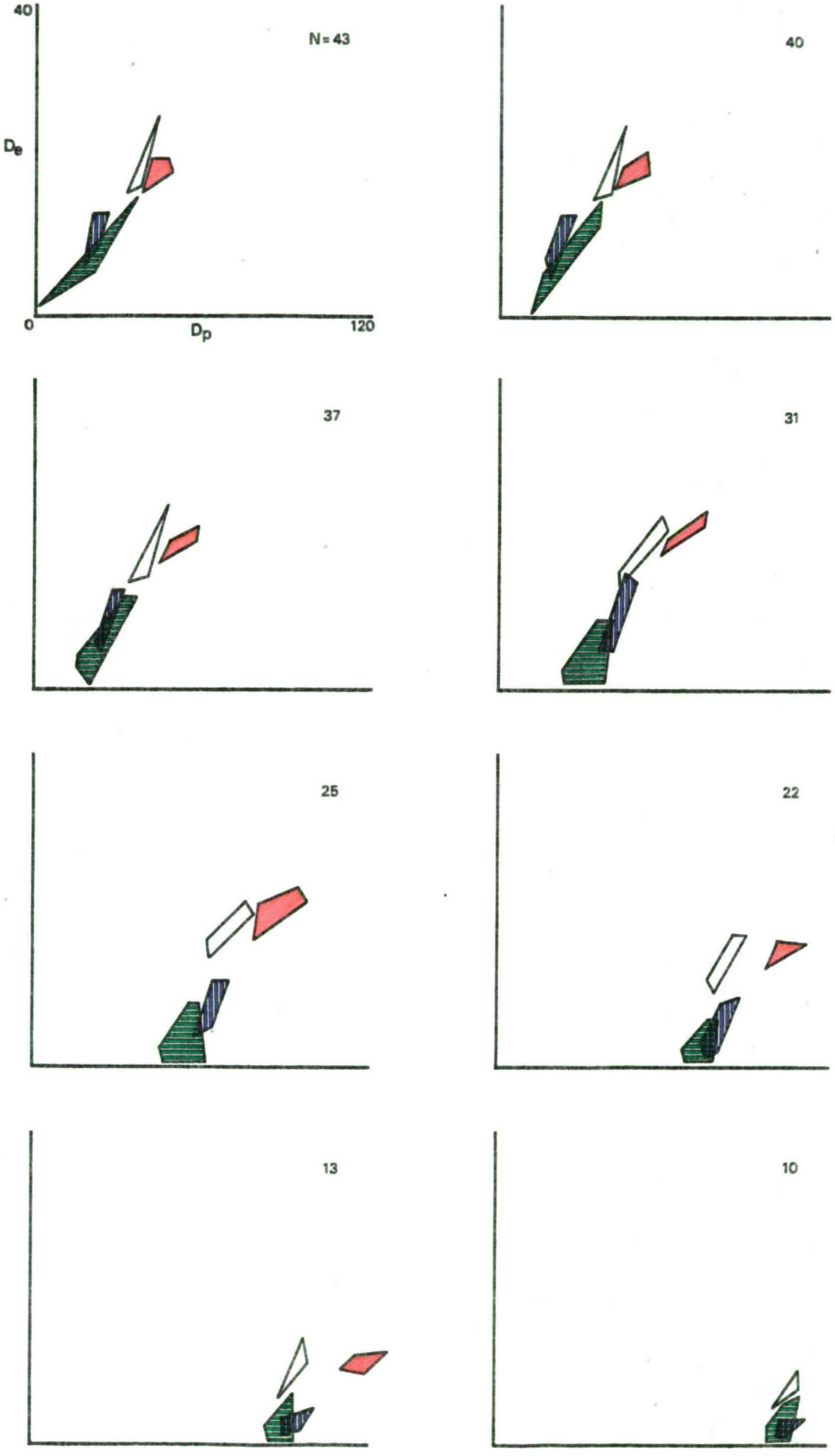
Deciduous forest.

Figure 5.46. Large-bodied species removed.

During this simulation there is comparatively little change in the relative positions of the four groups. The boreal group moves to the right relative to the deciduous forest group, but the semidesert group maintains its position relative to these two. Of the four groups, the tundra group shows the least increase in Dp values and hence the least movement towards the right. This group starts above and to the right of the two forest groups, and finishes directly above them by the end of the simulation.

The removal of large-bodied species reduces the overall similarity between the base fauna and modern communities, but it does not appear to significantly alter the relative similarity to communities from different modern habitats. At the end of the simulation, the structure of the base fauna shows more resemblance to the structure of tundra communities than formerly, but there is still an equal likeness to the structure of deciduous and boreal forest communities.

Figure 5.46.



Residual diversity simulations: Temperate habitats.

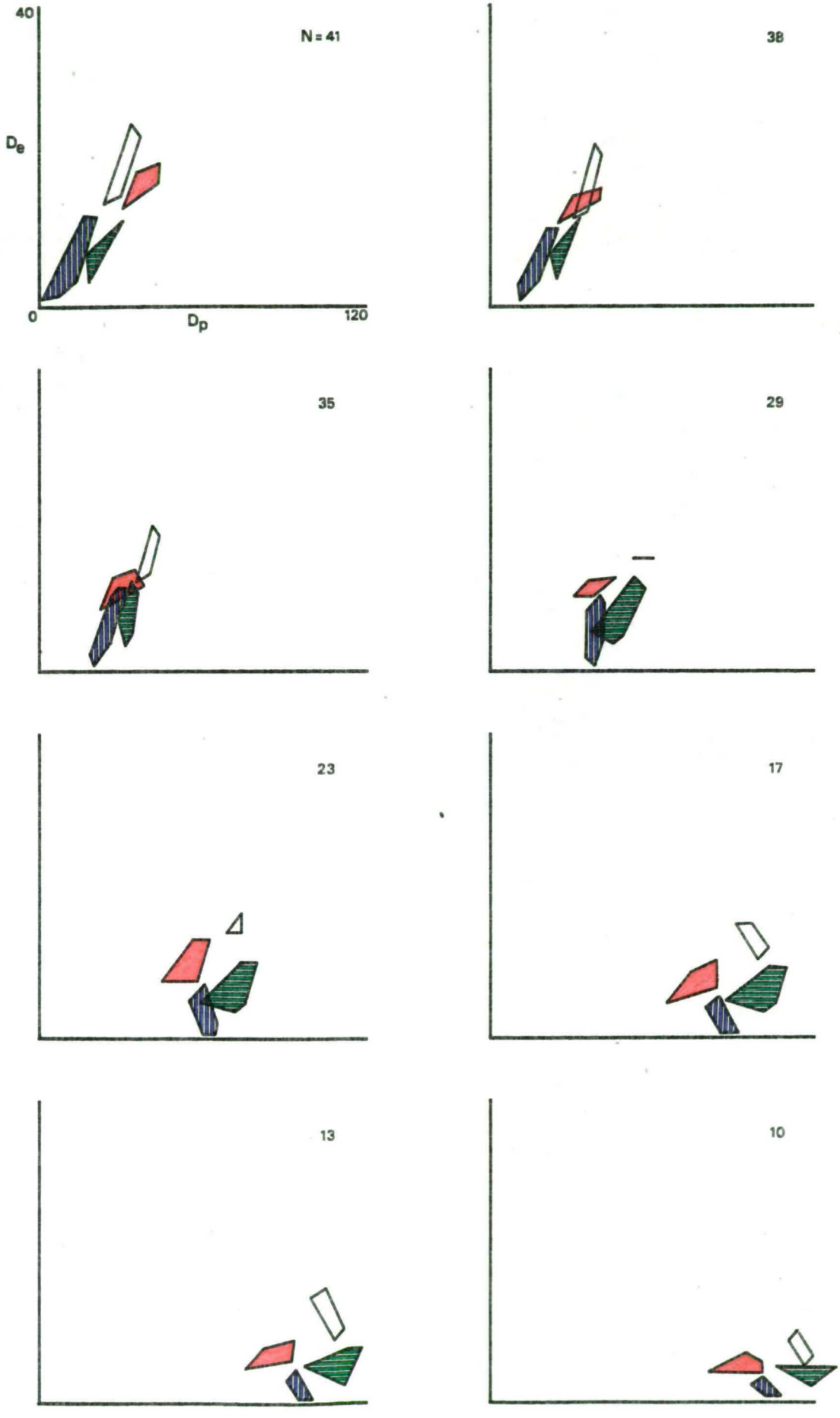
Boreal forest.

Figure 5.47. Small-bodied species removed.

During the general movement downwards and to the right, the relative positions of the two forest groups and the tundra group are maintained. The deciduous group lies to the right of the boreal group, while the tundra group stays above the deciduous forest group. However, while the relative positions of these three groups changes little, the semidesert group moves from a position on the right, where it is initially the most distant group from the origin, to finish lying nearest the origin with lower Dp values than the other groups.

In the unbiased state, the base fauna is most similar in structure to other boreal forest communities, but as small-bodied species are lost from the community, this similarity diminishes. The base fauna gradually becomes less like any of the modern communities, but the closest structural affinities by the end of the simulation are to be found in semidesert communities and boreal forest communities.

Figure 5.47.



Residual diversity simulations: Temperate habitats.

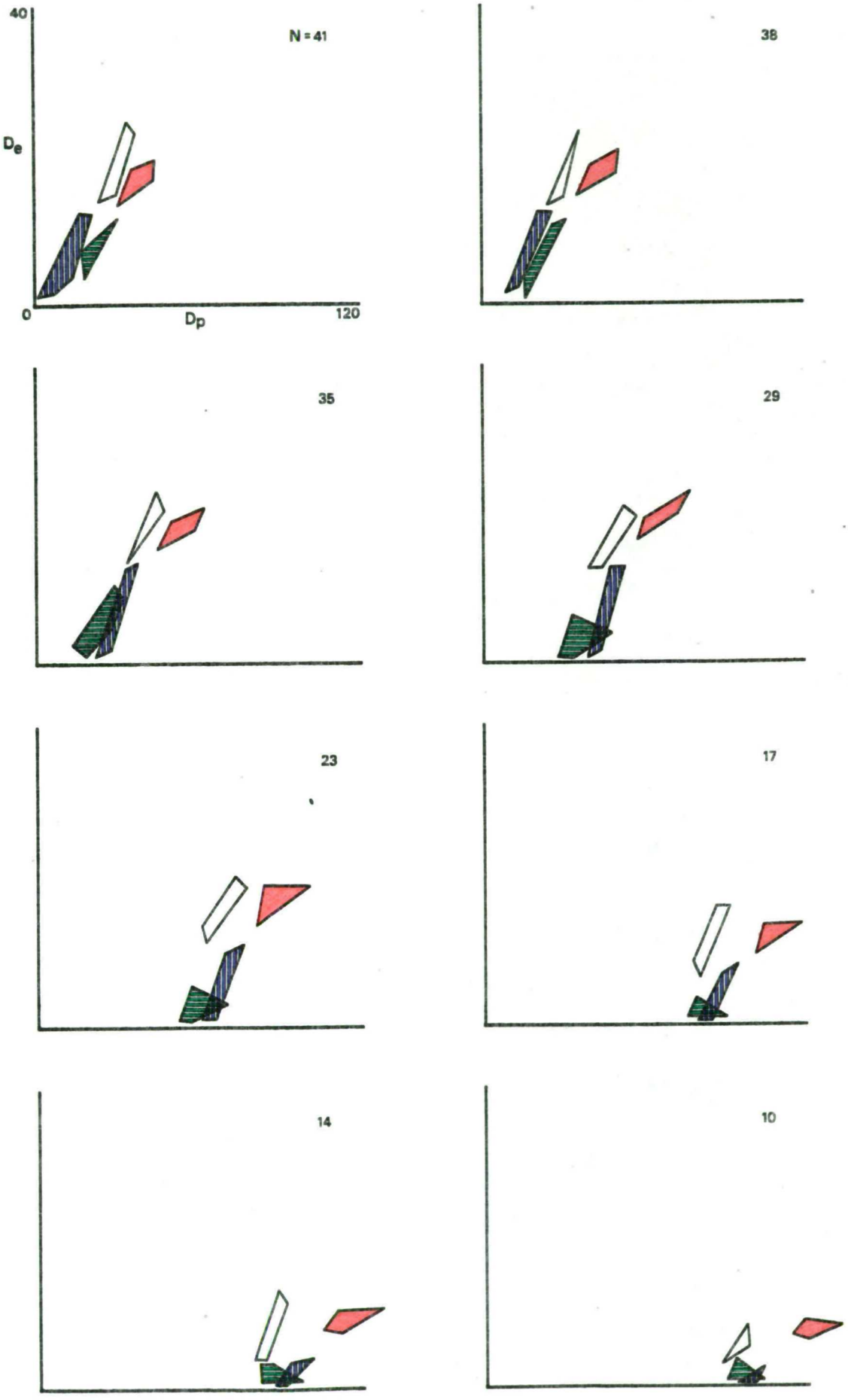
Boreal forest.

Figure 5.48. Large-bodied species removed.

Once again, all the habitat groups show a general trend downwards and to the right and during this general movement the deciduous forest group moves from a position on the right of the boreal group, to take up a position where it overlaps and lies partly to the left of the group of boreal forest communities. The tundra group maintains a position vertically above the deciduous group throughout. The semidesert group maintains De values similar to those of the tundra group, but it moves further to the right than the other three groups.

Before the removal of species, the base fauna is clearly most like communities from forest habitats and boreal forest in particular. The removal of large-bodied species from the base fauna gives it a structure less like that of boreal forest communities and more like that of deciduous forest and tundra communities.

Figure 5.48.



Residual diversity simulations: Temperate habitats.

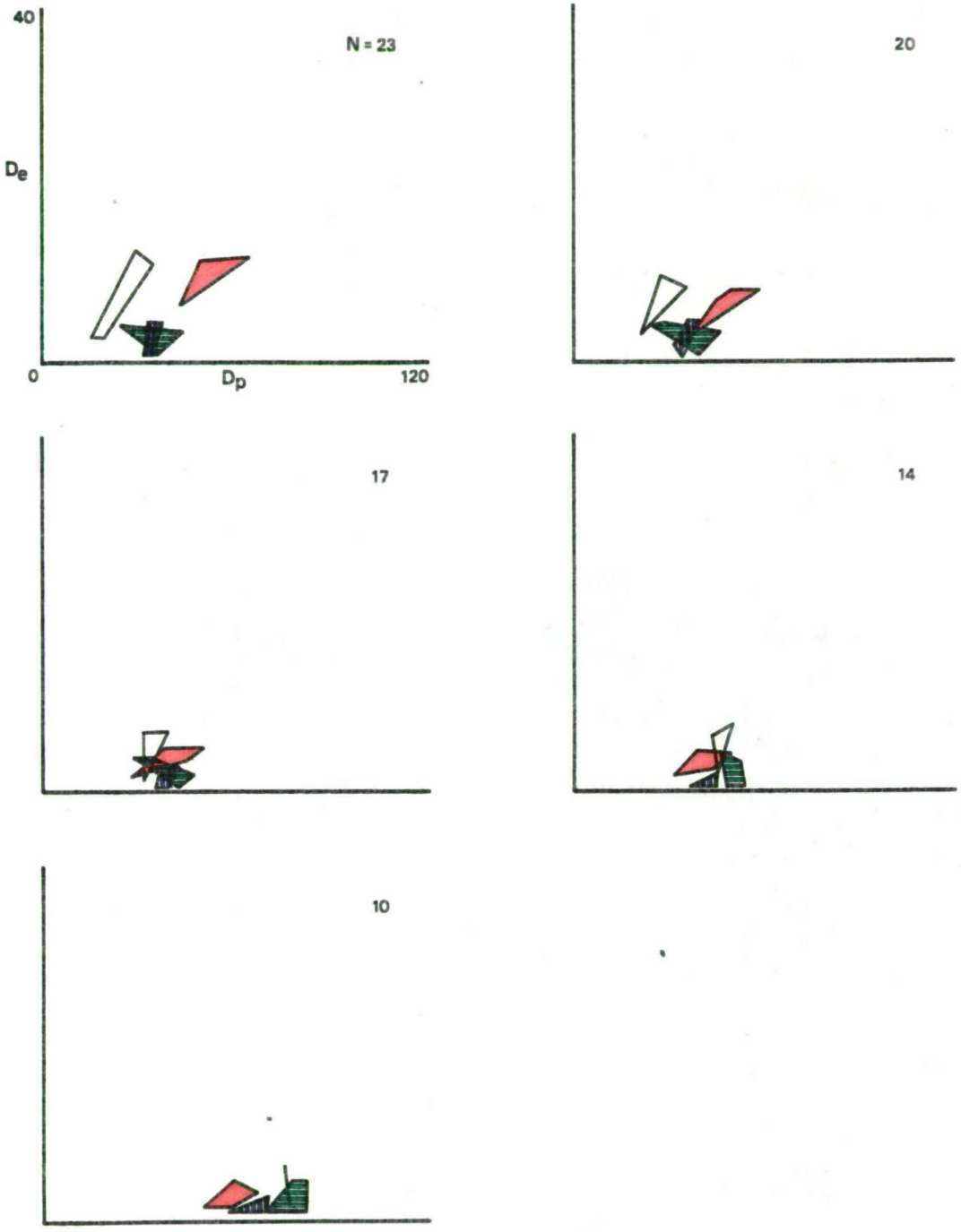
Tundra.

Figure 5.49. Small-bodied species removed.

Even with the removal of only 13 species from the base fauna, the residual diversity pattern changes dramatically. The tundra group, which starts to the left and largely above the two forest groups, shows a great deal of displacement to the right and finishes overlapping the deciduous forest group. The semidesert group, which initially is to the right and above the two forest groups, shows practically no rightward displacement, most of its movement being vertically downwards. It is crossed by the other three groups during the simulation, but finishes as the group nearest the origin. The forest groups overlap initially, but by the end of the simulation the deciduous forest group has shown a greater increase in Dp values than the boreal communities and lies to the right of the boreal forest group.

The removal of small-bodied species from the tundra base fauna reduces the similarity of its structure to tundra communities. The resemblance to boreal and deciduous forest communities is also reduced and by the end of the simulation the structure of the base fauna is most like that found in semidesert communities.

Figure 5.49.



Residual diversity simulations: Temperate habitats.

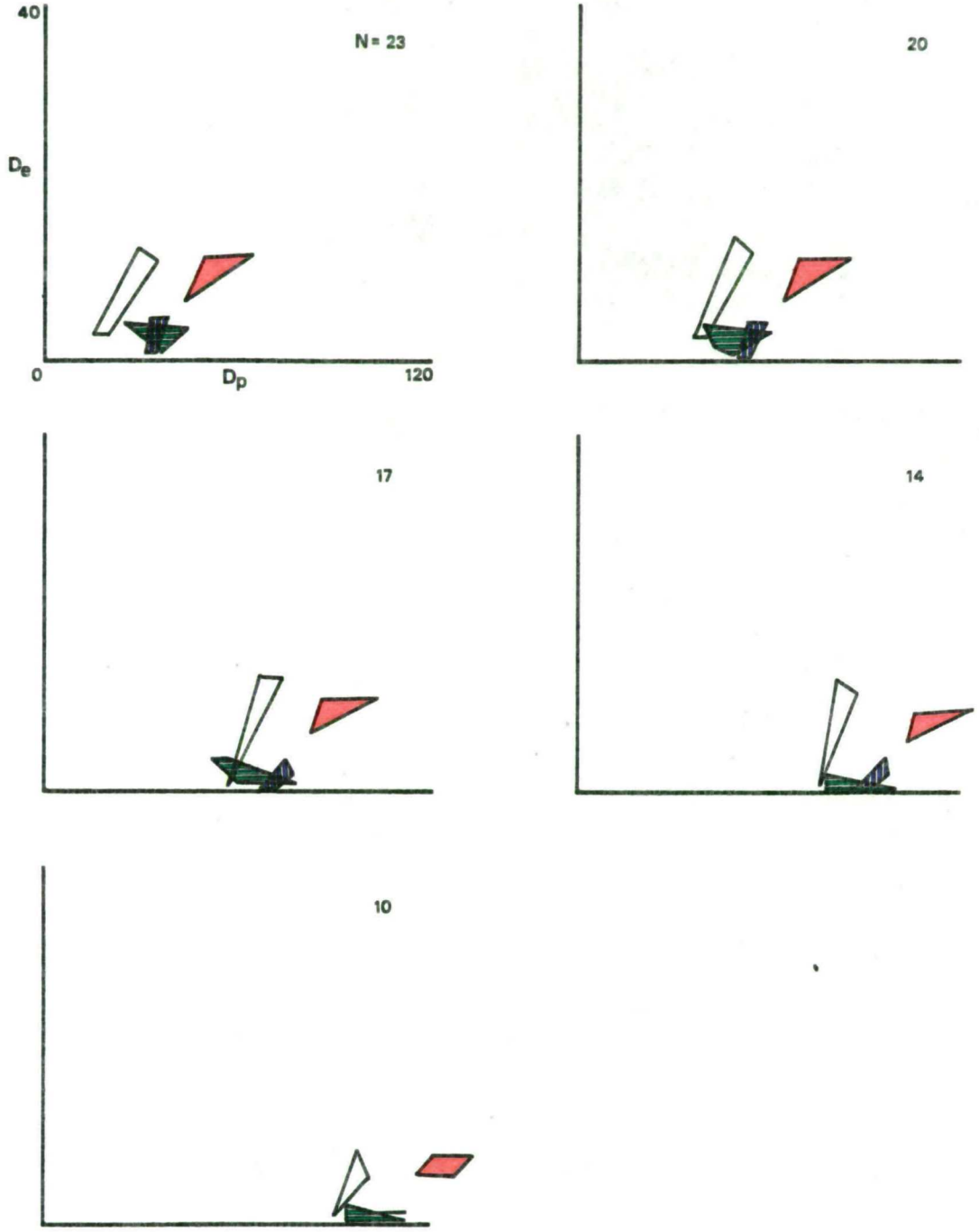
Tundra.

Figure 5.50. Large-bodied species removed.

Despite the usual displacement of all groups downwards and to the right, there is little change in the relative positions of the four groups. The two forest groups remain overlapping throughout. The tundra group stays above and to the left of these, while the group of semidesert communities remains above and to the right.

This simulation shows that the removal of large-bodied species from the tundra base fauna has very little effect on the affinities of the base fauna beyond reducing its overall similarity to modern communities.

Figure 5.50.



Residual diversity simulations: Temperate habitats.

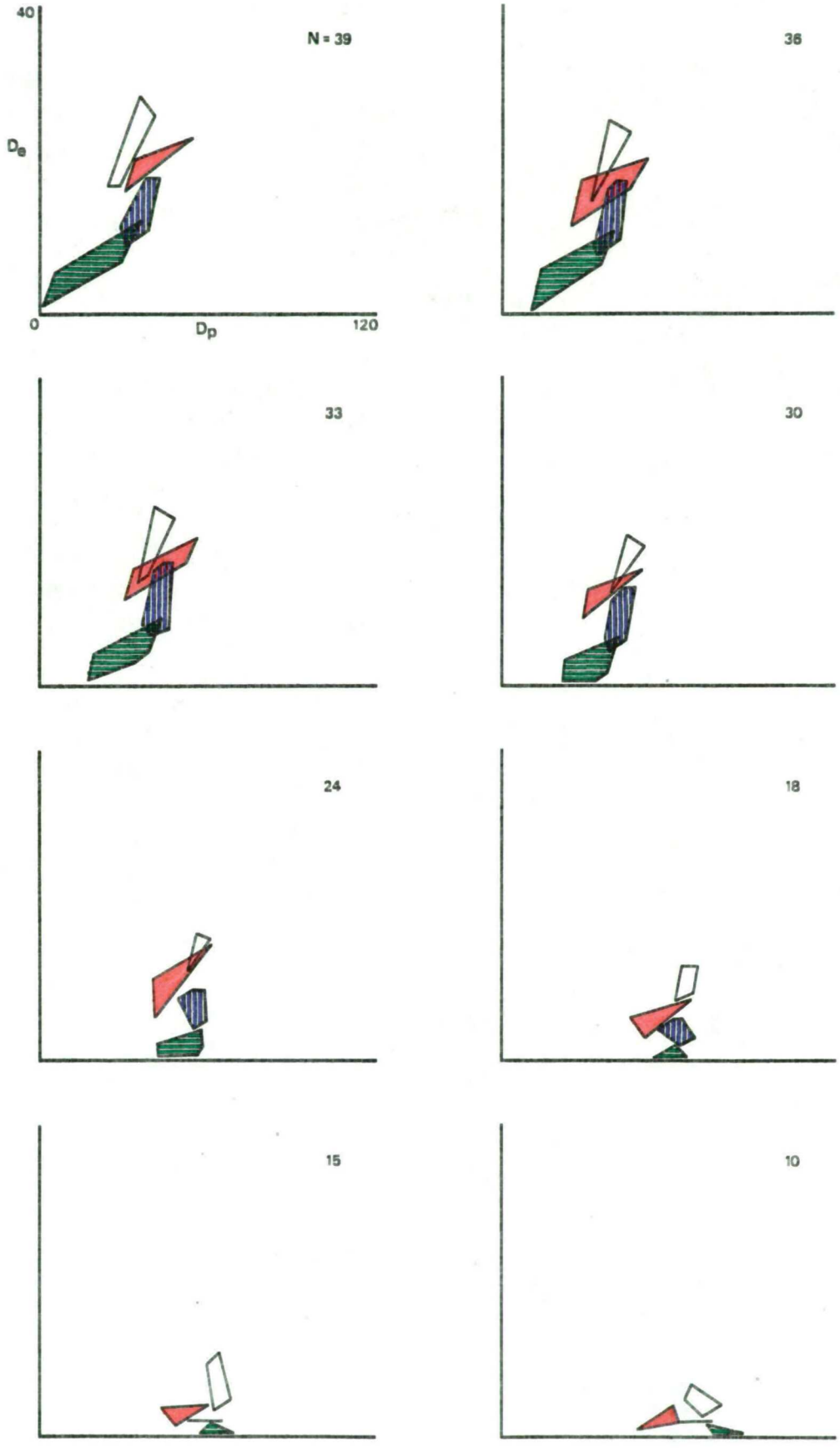
Steppe (forest-steppe).

Figure 5.51. Small-bodied species removed.

In the unbiased state the deciduous forest group is nearest the origin, with the boreal group overlapping the upper and rightmost part. During the course of the simulation the relative position of these two groups changes, the boreal group passing above the deciduous group until the latter lies the the right. The tundra group maintains its position above the two forest groups throughout. While these three groups all show a tendency to move away from the origin towards the right, the semidesert group, which starts to the right of the tundra group, shows practically no horizontal displacement. It drops almost vertically downwards and ends the simulation as the group nearest the origin, with the lowest Dp values of the four groups. All four groups share similar De values.

It can be seen from this simulation series that the removal of small-bodied species changes the structure of the base fauna from one which closely resembles that found in steppe, forest-steppe and deciduous forest communities, into one that has its closest affinities with semidesert communities.

Figure 5.51.



Residual diversity simulations: Temperate habitats.

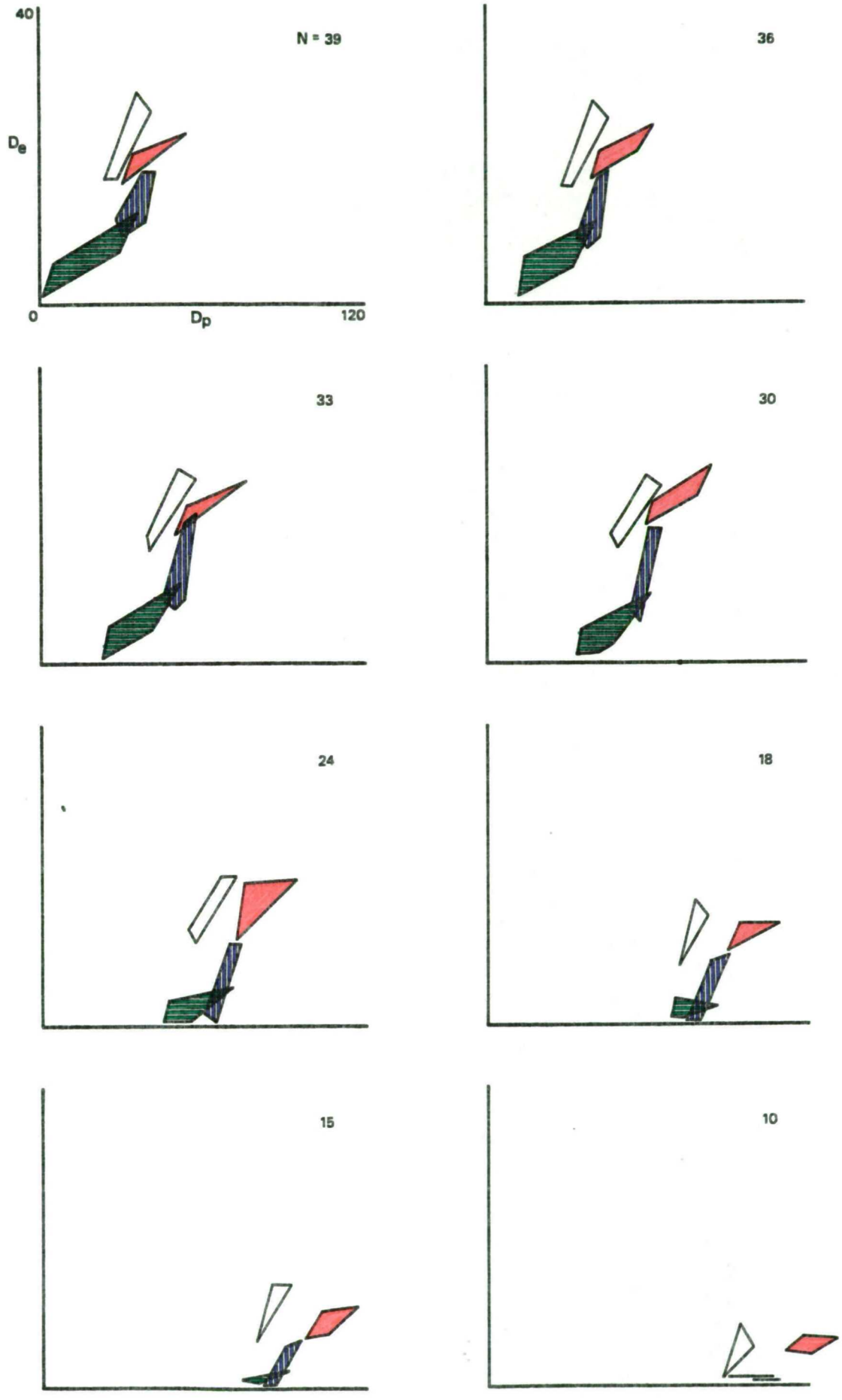
Steppe (forest-steppe).

Figure 5.52. Large-bodied species removed.

The relative positions of the four groups remain fairly constant throughout this simulation. The two forest groups share similar De and Dp values during the whole sequence, despite showing extreme vertical collapse towards the end of the simulation. The group of semidesert communities shows the greatest rightward displacement and moves from an initial position above the boreal group to finish to the right of the two forest groups. The tundra group shows the least movement towards the right and ends the simulation lying above the deciduous forest group.

The removal of large-bodied species decreases the overall similarity of the base fauna to modern communities, but does not seem to have much effect on the relative similarity to the four different habitat types. The base fauna continues to show some resemblance to forest communities, having a slightly greater affinity for deciduous forest throughout. The loss of large-species also makes the structure of the base fauna more similar to that found in tundra communities and less similar to that of semidesert communities.

Figure 5.52.



Residual diversity simulations: Temperate habitats.

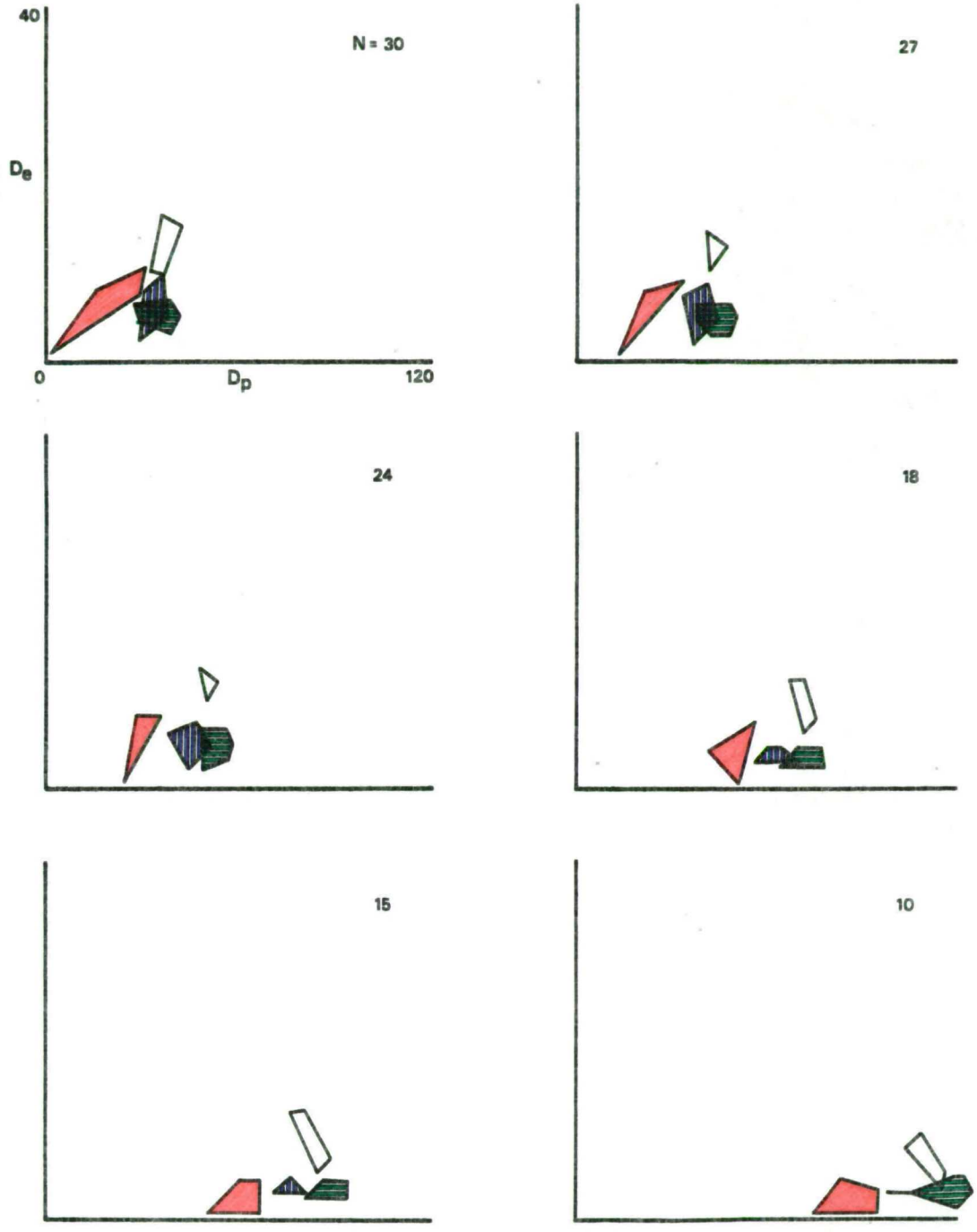
Semidesert.

Figure 5.53. Small-bodied species removed.

The relative positions of the four groups remain fairly constant throughout this simulation. The main characteristics of the unbiased pattern are preserved, with the semidesert group closest to the origin, the two forest groups to the right of this and the tundra group lying above the forest groups.

Although the base fauna gradually becomes less like any of the modern communties, the removal of small-bodied species evidently haslittle effect on the structure of the base fauna when compared to communities from different modern habitat types.

Figure 5.53.



Residual diversity simulations: Temperate habitats.

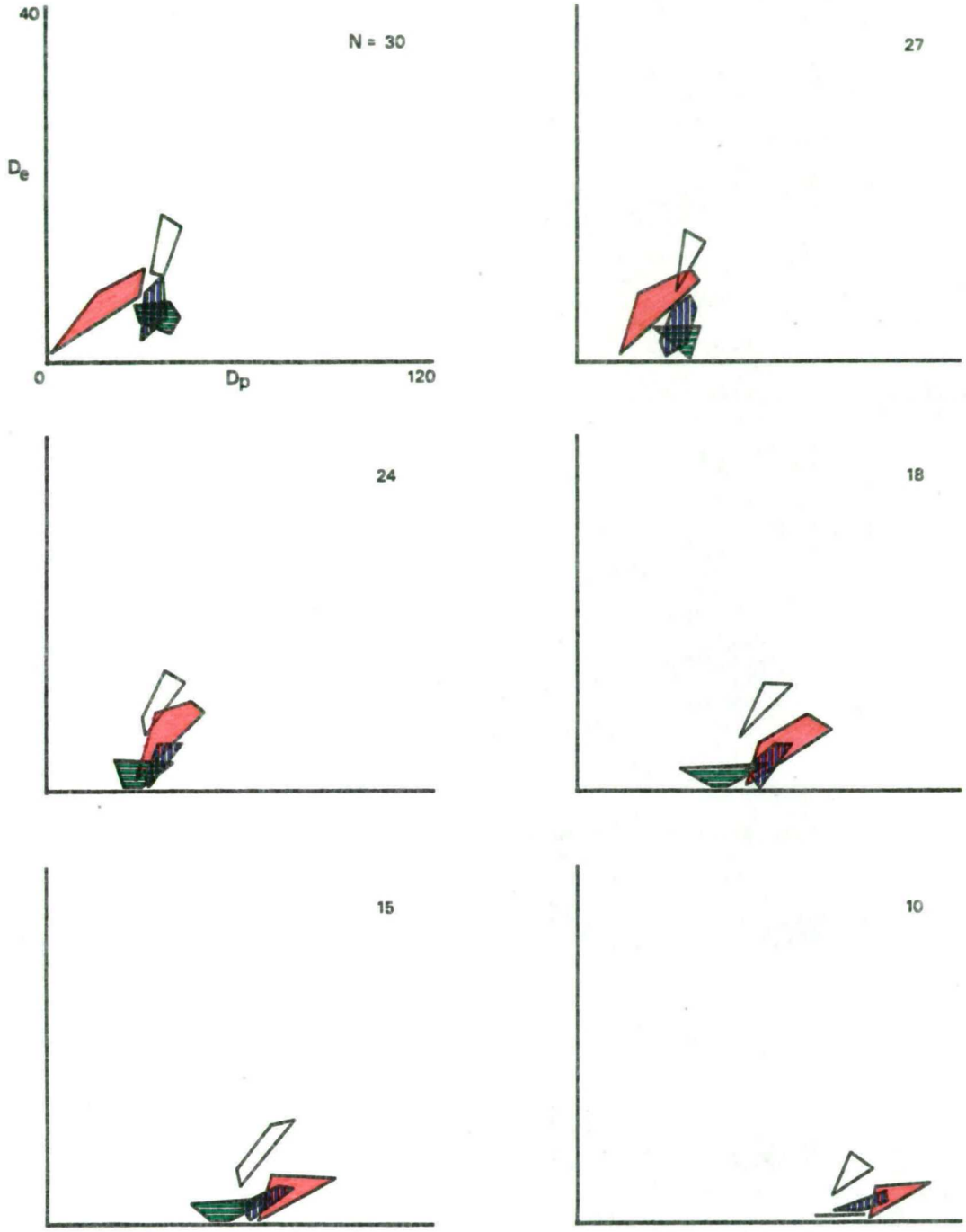
Semidesert.

Figure 5.54. Large-bodied species removed.

The relative positions of the four habitat groups changes considerably during this simulation. The semidesert group shows the greatest displacement to the right. It starts close to the origin and finishes furthest from the origin having crossed all the other groups during the course of the simulation. The relative positions of the two forest groups remains fairly constant and they intersect each other to some degree throughout. The group of tundra communities stays above the two forest groups during the whole sequence.

With the removal of large-bodied species, the base fauna gradually develops a structure which is less similar to modern communities overall, but relatively more similar to tundra and forest communities than to semidesert comunities.

Figure 5.54.



Conclusions.

Figures 5.55 and 5.56 show the final patterns resulting from the simulation series described above. Figure 5.55 illustrates the final patterns from the five series in which small-bodied species were removed, while figure 5.56 shows the final patterns resulting from the removal of large-bodied forms. It can be seen from these figures that the simulations tend to converge on two patterns. The removal of small-bodied species gives a base fauna dominated by large-bodied species. The residual diversity pattern of this kind of base fauna is most similar to that of semidesert communities (compare figure 5.55 with figure 5.44). The removal of large bodied species results in a base fauna whose residual diversity pattern shows most resemblance to those of tundra communities (compare figure 5.56 with figures 5.42, 4.1 and 4.2). Table 5.2 summarizes the effects of the two types of simulation on communities from five temperate habitat types.

Figure 5.55. Residual diversity simulations: Temperate habitats: Final patterns resulting from the removal of small-bodied species.

The final patterns resulting from the simulations in which small-bodied species were removed are shown. All five simulations converge on a final pattern which is most similar to that for semidesert communities, in which the semidesert group is closest to the origin, the boreal forest group lies nearer the origin than the deciduous forest group, and the tundra group lies above the deciduous forest group.

Figure 5.55.


40
$D_e$
0
$D_p$
120
Deciduous forest
Boreal forest
Tundra
Steppe
Semidesert

Figure 5.56. Residual diversity simulations: Temperate habitats: Final patterns resulting from the removal of large-bodied species.

This figure shows the final residual diversity patterns of the five simulations in which large-bodied species were removed. These five simulations all converge on a final pattern which is most similar to that for unbiased tundra communities. This is a pattern in which the tundra group is closest to the origin, or lies above the two forest groups, which also overlap in most cases. The semidesert group is furthest from the origin.

Figure 5.56.

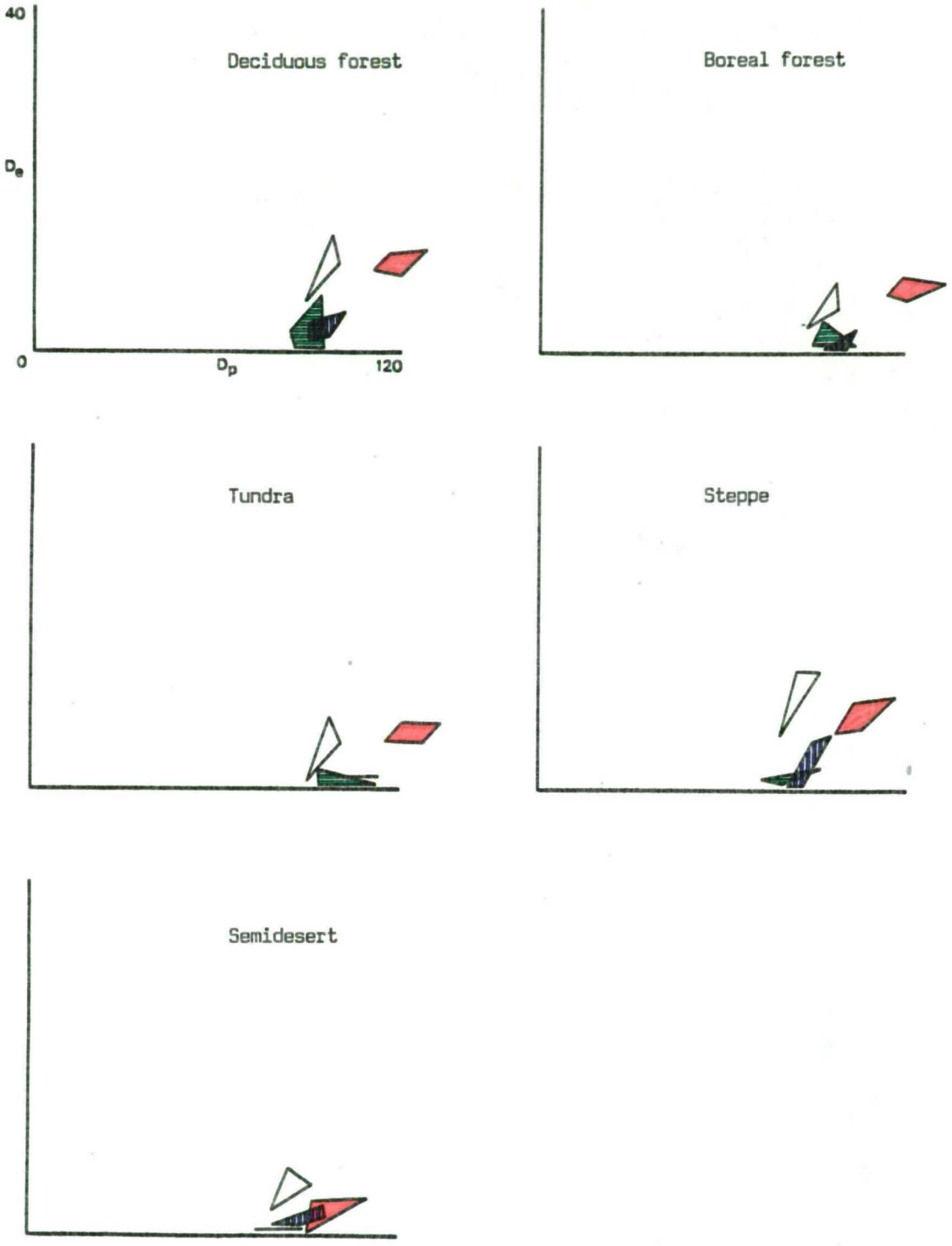

40
$D_e$
0
$D_p$
120
Deciduous forest
Boreal forest
Tundra
Steppe
Semidesert

Table 5.2. Effects of simulations on temperate habitats.

| Unbiased pattern type | Species removed | Species dominant in final fauna | Final pattern type |
|---|---|---|---|
| Deciduous forest | Small | Large | Semidesert |
| Deciduous forest | Large | Small | Tundra |
| Boreal forest | Small | Large | Semidesert |
| Boreal forest | Large | Small | Tundra |
| Tundra | Small | Large | Semidesert |
| Tundra | Large | Small | Tundra |
| Steppe | Small | Large | Semidesert |
| Steppe | Large | Small | Tundra |
| Semidesert | Small | Large | Semidesert |
| Semidesert | Large | Small | Tundra |

## 4. Conclusions from simulation studies.

Each modern habitat type has a distinctive THI and residual diversity pattern in the unbiased state, but the simulations described above show that these two palaeoecological methods respond in different ways to the loss of species.

The Taxonomic Habitat Index shows relatively little change as species are lost from a community. This appears to be irrespective of whether the species lost are large or small-bodied, and the observation applies at both the specific and generic levels. It can be concluded from this that THI patterns are influenced by taphonomic biases. However, it is known that the method is affected by taxonomic distance and that patterns become less distinctive with increasing geological age as the average degree of relatedness between fossil and modern taxa decreases. The use of THI is consequently more suited to recent faunas, but is not affected by species richness (or by geographical origin).

As far as Residual Diversity is concerned, the simulations corroborate the general predictions of the model presented in chapter 3. Species loss has a marked effect on residual diversity patterns, but these effects are predictable. In the simplest terms, the

residual diversity pattern of an unbiased community is determined by the kind of species which are dominant before species loss, while the final pattern of a simulation series is determined by the kind of species that are dominant after the loss or removal of species. The relationship between the unbiased and final patterns, expressed by the intermediate patterns of the simulation sequence, is controlled by the nature of the species that are lost from the community.

In practice, faunas with little species loss can be placed in the correct simulation type and the original habitat of the community identified. Extreme loss of species makes this impossible since the residual diversity pattern then gives very little indication of the original structure of the community. Even when some residual structure appears to be preserved, this is never sufficiently distinctive to allow the fauna to be definitely assigned to any particular habitat type.

Between the two possible extremes of species loss there is a possibility of identifying the habitat of the original community which depends on the degree and pattern of species loss. The chance of identifying the original habitat decreases as the degree of species loss increases. It also has to be observed that the simulations deal with completely non-random loss of species, which is a situation that will only rarely be encountered in the fossil record.

To summarize, unbiased communities have patterns that are entirely distinctive, whereas heavily biased faunas give patterns that are practically indistinguishable. The distinctiveness of these residual diversity patterns gradually decreases as the degree of taphonomic bias increases. These characteristics make Residual Diversity best suited to the analysis of communities with high species richness (e.g. tropical communities), but of any geological age.

There is also the possibility, not explored in the simulations in this chapter, that during the fossilization of a community, species from other communities could be added to the assemblage. At the same time there is also the possibility of encountering a community originating in a habitat not represented in the sample of modern communities. It is to be expected that fossil faunas derived from communities inhabiting environments that do not exist today will have ecological structures different from those of modern communities represented in the modern comparative sample. However, since the initial pattern before species loss is determined by the structure of the community, and this initial pattern itself determines the appearance of any patterns resulting from species loss, then these communities should be distinctive even under the influence of taphonomic biases. Finally, it also has to be considered that what might at first be

interpreted as a habitat not represented in the modern sample, could actually be a sere or an edaphic climax rather than an idealised climatic climax. This is a problem that is always likely to affect parochially based reconstructions particularly seriously and it is important in the light of this observation that the analysis of any fossil fauna should use as many palaeoecological methods as possible.

Chapter 5: Summary.

Chapter 5 investigates the response of two palaeoecological methods (Taxonomic Habitat Index and Residual Diversity) to the loss of species from an original community.

Fossilization is a chancy process and in most cases a fossil fauna is an incomplete representation of the palaeocommunity from which it is derived. The effect of incomplete preservation on different palaeoecological methods are explored by simulating taphonomic biases.

The unbiased THI and residual diversity patterns of one community from each of the modern habitats described in chapter 4 are illustrated. Each community is then subjected to two simulations, firstly, the removal of small-bodied species and secondly, the removal of large -bodied species. The THI and residual diversity patterns for each community were re-drawn at stages during the simulations to show how each method is affected by the loss of species from the community.

It is concluded that THI patterns are relatively insensitive to the loss of species, whereas residual diversity patterns change dramatically, but predictably, in such a way that the chance of identifying the original habitat decreases as the degree of species loss increases.

As an overall conclusion it is seen that THI is affected by geological age, but not by taphonomic factors, while Residual Diversity is affected by taphonomic biases, but not by the geological age of the fauna. As a consequence, THI is best suited to more recent fossil faunas, irrespective of species richness, whereas Residual Diversity is better suited to the analysis of faunas containing many species, irrespective of the age of the fauna.